Nutrients as a Factor in Food Selection by Captive Wild Herbivores

Inaugural-Dissertation

zur Erlangung der Philosophischen Doktorwürde
vorgelegt der
Philosophischen Fakultät
der Universität Zürich II

von
MORITZ RUSTERHOLZ
von Zürich

Begutachtet von

Daniel H. Janzen
Professor of Biology
University of Pennsylvania

und

Prof. Dr. Hans Kummer

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Abstract

Aims and mechanisms of food selection are discussed in the introduction. In order to elucidate the role nutritional properties of food plays in food selection, multiple food choice experiments were performed. Arabian oryxes (*Oryx leucoryx*) and South African oryxes (*Oryx beisa*), kept at the Zoological Garden of Zurich, Switzerland, served as test animals. As test foods, different pellets of known composition were offered *ad libitum* together with a limited amount of alfalfa hay or meadow hay and carrots, respectively. Every day and for each animal, the consumption of each food type was recorded. Food characteristics were tested for their relevance in food selection. Using nutritional constraints and different objective functions (maximization of energy, protein or nitrogen free extracts [NFE], respectively, minimization of fiber) linear programs were established. By comparing these theoretical diets with the effective diets it was possible to show that one theoretical diet was more similar to the effective diets than others. In most cases it was that theoretical diet with fiber minimization, somewhat less frequently that diet with NFE maximization. The results are discussed with respect to the importance of nutritional food properties in food selection.

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1. Introduction

It is obvious that every animal exhibits food selection. Consider two main selective pressures on this behavior: 1. Toxins avoidance. Both in the animal kingdom and in the plant kingdom, toxins are a common defense against consumers. Although many consumers have specific detoxification mechanisms, many more prey species will remain toxic for them. Thus it is preferable to recognize the edible food-stuffs and to avoid the toxic ones, i.e. to exhibit food selection. 2. Food input according to bodily needs. To remain healthy the animal needs nutrients, i.e. proteins, fats, carbohydrates, major minerals, trace elements, and vitamins in specific amounts. Not everything that is nontoxic and edible is of nutritive value. An animal can starve with a stomach full of food-stuffs if these are indigestible (MOEN, 1973); it is therefore necessary to be able to distinguish between nutritive and non-nutritive food-stuffs. Again the result is food selection.

Even among the nutritive food-stuffs, the animal should be selective. In consuming only one food type, the animal will rarely meet all its nutritional needs. Even the monophacic coala bear needs leaves from more than one individual eucalyptus tree (FIRTH, 1973). In carnivorous mammals relatively few prey species make up the bulk of the diet

and the rest are eaten only occasionally. The typical diet of herbivorous mammals is more diverse, and the diets of omnivores, e.g. rats and man, exhibit an even larger variability.

The widespread existence of food selection is an undisputed fact. However, the mechanisms of food selection and the criteria by which an animal selects a food item are disputed and have recieved a great deal of attention. By way of introduction, J have summarized below the most important concepts on this theme currently found in the literature. Their relevance to the research reported here will soon become evident.

1.1 Aims and mechanisms of food selection

A relatively old concept in food selection is that of "nutritional wisdom" (RICHTER, 1943). This concept combines both above-mentioned goals of food selection, namely toxin avoidance and food intake according to nutritional requirements. Originally, nutritional wisdom implied that animals select their foods in such a way that the resulting diet optimizes their nutritional well-being; they avoid eating poisonous and nutritionally poor foods. However it is clear that animals are not capable of selecting their foods every time in perfect accordance with their nutritional requirements, and the existence of body reserves suggest that a "perfect" food

selection may not even be necessary or possible (or that food is periodically unavailabel to chose from). Nevertheless one can reformulate the concept of "nutritional wisdom" as follows: an animal shows "nutritional wisdom" when the sum of the foods consumed daily lacks lethal amounts of poisonous substances and if the resulting nutritive input matches the actual nutritional requirements as well as possible (though not necessarily perfectly). WESTOBY (1974) calls this theory, "fallible nutritional wisdom".

1.1.1 Appropriate food intake

The concept of "nutritional wisdom" itself does not explain any underlying mechanisms and only postulates the existence of a mechanism leading to poison avoidance and appropriate food intake. Assuming that appropriate food intake is fallible, the animal should possess mechanisms to detect nutritional deficiencies caused by inappropriate food intake or by periodically unavailable foods and mechanisms to correct these. One such mechanism could involve the formation of "specific hungers", postulated by RICHTER (1943), ALBRECHT (1945), and others.

SCOTT & VERNEY (1949) tested rats suffering from thiamine deficiency. These rats showed a preference for diets containing as little as 0.1ppm (and up to 1000ppm) of thiamine. But the rats' selection was not errorless and they showed this preference only when they were seriously

thiamine-deficient. SCOTT & VERNEY concluded that the specific hunger for thiamine was a learned behavior and not innate. RODGERS & ROZIN (1966) confirmed this with their experiments on rats: they offered thiamine-deficient rats a novel diet without thiamine and simultaneously, the familiar diet on which they had become deficient, but now enriched with thiamine. Here, the rats selected the novel diet and did not react to the thiamine-increase in the familiar food. The aversion to the ill-making food, learned by association, overcame an innate neophobia. ROZIN (1967a) offered thiamine-deficient rats the familiar food and a novel food, both lacking thiamine. Also in this experiment, the rats immediately preferred the novel food over the familiar one. And lastly, RODGERS (1967b) offered thiamine-deficient rats two novel foods, one of them containing thiamine. The rats were not able to immediately select the thiamine-containing food, but in time, did prefer the enriched food. Obviously rats can not detect thiamine *per se*. All these findings show clearly that a specific hunger for thiamine must be learned. The same is valid for calcium and for the specific aversion to magnesium (RODGERS, *op cit.*).

Different results were obtained with sodium-deficient rats. NACHMAN (1962) found that adrenalectomized rats showed immediate preference for sodium-rich foods. DENTON (1965), RODGERS (1967), ROZIN (1967b), and others also conducted experiments with sodium-deficient animals,

and all results support the conclusion, that a specific hunger for sodium is one example of innate nutritional wisdom. RODGERS(1967) attempted to explain this exception: Because sodium is of great importance in the maintenance of osmotic balance, an immediate correction of imbalance is desirable. Besides this, a learned sodimum hunger could lead to an oscillation between hypotonicity and hypertonicity with a more slowly acting mechanism; and lastly, sodium-deficiency is as detrimental as sodium-excess. For the same reasons, a specific hunger for water is also thought to be an innate mechanism (ROZIN, 1967a).

Another possibility for attaining appropriate food intake involves the mechanism of "long-delay learning". This is learning with a long delay between the conditioned stimulus (CS) and unconditioned stimulus (UCS). Long-delay learning mechanisms were first discovered in experiments on food aversion learning (GARCIA *et al.*, 1966; REVUSKY, 1968; and others). Some specific hungers can be explained by long-delay learning mechanisms, in that a food which produces recovery effects represents the long-delayed UCS (SCOTT & VERNEY, 1949; ROZIN & KALAT, 1971). It is assumed with this mechanism, that some sensory property (-ies) of the food, e.g. smell, taste, sight are stored centrally. In this way it is possible to associate the recovery effect with that food even after a long delay.

Theoretically, such associations could also be made between nutritional properties of a food - recorded by proprioreceptors during digestion - and the stored sensory properties of that food. Such an ability would be a powerful tool for selecting nutritionally appropriate foods, because one or a very few trials would suffice to produce learning, and it would enable the animal to identify the nutritive characteristics of a known food before ingestion.

For long-delay learning to function properly, only one novel food can be ingested at a time, otherwise an association between sensory and nutritional properties of that food is not possible. Indeed, investigations have revealed that animals eat only one novel food at a time (ROZIN, 1967a, 1967b; MUERI, 1978). Although long-delay learning undoubtedly exists, the basic mechanisms are largely hypothetical. Furthermore, long-delay learning with respect to diet optimization, as WESTOBY (1974) proposes for large herbivores, has to my knowledge not yet been investigated.

A third possible mechanism for appropriate food intake has beed proposed by ZAHORIK & HOUPT (1971), namely "mixed food behavior". The idea was developed especially for grazing animals, and put forth the possibility of innate behavior to feed on different foods in moderate amounts. As many investigations have demonstrated, most

grazing animals show a clear tendency to eat a variety of different foods every day (STEWARD, 1971; SZMIDT, 1975; TEN HOUTE DE LANGE, 1978; VOSER-HUBER, 1975; and others). This behavior could lead to a fairly well-balanced diet, under the assumption that the potential foods in a habitat can offer a well-balanced diet. If all potential foods are similarly insufficient with respect to a nutrient, or if there is a shortage of available foods, malnutrition is inevitable. The same strategy, i.e. the choice of several feeds in a meal, could also lead to poison-avoidance (discussed in detail below) since the toxicity of all substances is related to concentration. A correlate of this model from ZAHORIK & HOUPT is the preference for leaves and new-growth, which is thought to be innate. Leaves and new-growth contain more gross energy and protein, and less fiber, fewer tannins and other secondary compounds than stems and older plant part. Because of this, the preference for leaves and new-growth would automatically lead to a nutrient-rich and secondary compound-poor diet.

1.1.2 Poison avoidance

As with appropriate food intake, various mechanisms have been proposed to explain poison avoidance. The first postulated mechanism is that of "food aversion learning". Here, if an animal eats a food which makes it sick, the

animal correctly associates the aversive stimulus with taste or other sensory cues of the food, responsible for the illness. The suitable learning form would be "long-delay learning", since at least several minutes pass between ingestion and onset of digestion. The fact that gastrointestinal aversive stimuli are always associated to taste (foods) is a principle called "belongingness" (GARCIA & KOELLING, 1966). The "novelty-principle" (REVUSKY & BEDARF, 1967) further states that illness will be associated to novel foods rather than to familiar ones, and becomes important whenever a novel food is eaten together with familiar foods.

Food aversion learning would not be useful if this illness were to be associated with familiar foods. "Mixed food behavior" (ZAHORIK & HOUPT, 1977) would not only lower the intake of poisons as discussed earlier, but also be advantageous in situations of food shortage: an animal that avoids poisoning by food aversion learning will starve if not enough "acceptable" food is available, whereas an animal with "mixed food behavior" could nourish itself much longer.

The concept of the "mixed food behavior" although appealingly simple and effective, does have its limits: What would happen if the toxicity of a food is so high that even a small amount could kill the consumer? One possible solution would involve the capability of the

animal to inactivate the toxic substances. Such detoxification mechanisms are known to exist: one acts through microsomal enzymes which are located on the endoplasmatic reticula. Another system is found in the alkaline stomach where the microbial and protozoan populations can degrade multiple kinds of secundary compounds. For both detoxification systems "experience" with a particular secondary compound is eminently important.

With respect to the microsomal enzymes, an animal possesses no complete set of enzymes (FREELAND & JANZEN, 1974), and even those which are present, occur only in low concentrations. If, under these circumstances, a toxic food is consumed in large amounts, the detoxification system will be overloaded and the poison can be damaging. If, on the other hand, the toxic food is introduced carefully in small amounts, the poison will induce and accelerate the synthesis of a specific microsomal enzyme.

With respect to detoxification in the alkaline stomach, especially in the rumen, it is thought that the bacterial and protozoan flora will selectively alter, if a toxic food is introduced carefully enough. Those strains of bacteria and protozoa which are capable of living with, and/or degrading the toxic substances, will survive (FREELAND & JANZEN, 1974).

It is important that herbivores recognize poisonous substances either directly or indirectly, by association with accompanying characteristics. CHAPMAN & BLANEY (1979) assume that the avoidance or acceptance of a food, based on its content of secondary compounds, is mainly innate. FREELAND & JANZEN (1974) however, stress the importance of learning in poison avoidance, but do not deny the possibility of innate behavior in this area. One can assume that in those cases where direct perception of the poison occurs, innate responses have evolved; otherwise the direct perception need not have evolved.

Both poison avoidance mechanisms referred to, neophobia coupled with learning, and "mixed food behavior", require that only a small amount of a potentially poisonous food be consumed. Whereas learned food aversion leads to a complete avoidance of a poisonous food, the innate "mixed food behavior" allows limited consumption of this food. Furthermore, "mixed food behavior" can be used to explain those cases where a poisonous food is consumed in relatively large amounts: this could happen when food diversity slowly lowers, and the animal is forced to consume larger amounts of each food. During this process, the detoxification mechanisms could adapt to the greater toxin burden.

Aside from secondary compounds, major minerals, trace elements and some vitamins act as poisons when over-con-

sumed. Even main nutrients can harm the organism by impairing digestion if they are ingested in excess. On the other hand, most main nutritive substances and even minor nutrients induce deficiency diseases if ingestion falls below their critical values. Thus, an animal needs not only to avoid specific food items, but also has to search for specific foods. And, in order to arrive at a proper diet, this should be done in such a manner that the ingested foods contain the needed nutrients in appropriate amounts (neither too much, nor too little), and lack harmful amounts of secondary compounds. The result of such a food selection is an optimal diet but not necessarily maximum fitness.

1.2 Diet optimization

Mechanisms which lead to diet optimization bring the animal a great selective advantage because an optimally nourished animal is highly resistant against infections of all kinds. Thus, the existence of diet optimization mechanisms in animals is a reasonable assumption, even if they place high demands on the animals.

Realizing that energy takes a key position in nutrition, most models aim at maximization of energy intake per unit time, either by minimizing the energy expenditure on food search and food handling or by maximization of gross energy yield (McARTHUR & PIANKA, 1966; EMLEN, 1966; EMLEN & EMLEN, 1975; RAPPORT, 1971; SCHOENER, 1971; MARTEN, 1973; PULLIAM, 1974; WILSON, 1976). In all of these works,

nutrient constraints are not allowed. But because nutrient constraints do exist everywhere and have a great influence on diet optimization, it was important to develop models which take these into account. Therefore, WESTOBY (1974) proposed the use of a linear program model, analogous to those applied in computing a feeding regime for penned livestock or other domesticated animals. There, the objective function in the linear program is the minimization of financial costs; WESTOBY (*op cit.*) chose energy maximization as his objective function. Knowing the nutrient constraints placed upon an animal, linear programs allow the calculation of optimal diet under different objective functions for a given food set.

At the time of my dissertation research, this method had not yet been applied to the study of herbivore feeding behavior in "real life", and I proposed its use to determine whether a herbivore selects its diet according to a particular nutritional "strategy". The underlying theory is, of course, that of "fallible nutritional wisdom" (WESTOBY, 1974).

"Mixed food behavior" (ZAHORIK & HOUPT, 1977) can also be thought of as a model for diet optimization. It assumes an animal which is well adapted to a given environment and eats a multitude of different foods with few preferences. If this animal is able to avoid highly toxic plants, it is plausible that this behavior may lead to

optimized diet automatically. Whereas this model may result in an optimal diet only if the animal is well adapted to its environment, the model based on "fallible nutritional wisdom" is apt to optimize the diet under any conditions; this makes the latter more attractive and is why I chose to assume fallible nutritional wisdom as the starting point for my investigations.

To this point, I have introduced ideas on food selection in general; by way of background information for my own research presented later, I shall now restrict the discussion to the ruminants. The animals are particularly interesting since most are large generalist herbivores which feed on somewhat less nutritious vegetation than their non-ruminating counterparts.

2. Feeding behavior of the ruminant

The current state of knowledge on ruminant food selection, nutritional requirements, food-intake regulation and possible diet optimization mechanisms is presented in the following sections.

2.1 Food selection

In Fig.1, I have attempted to summarize the variables thought to influence food selection by ruminants.

Food selection itself takes place with the aid of the

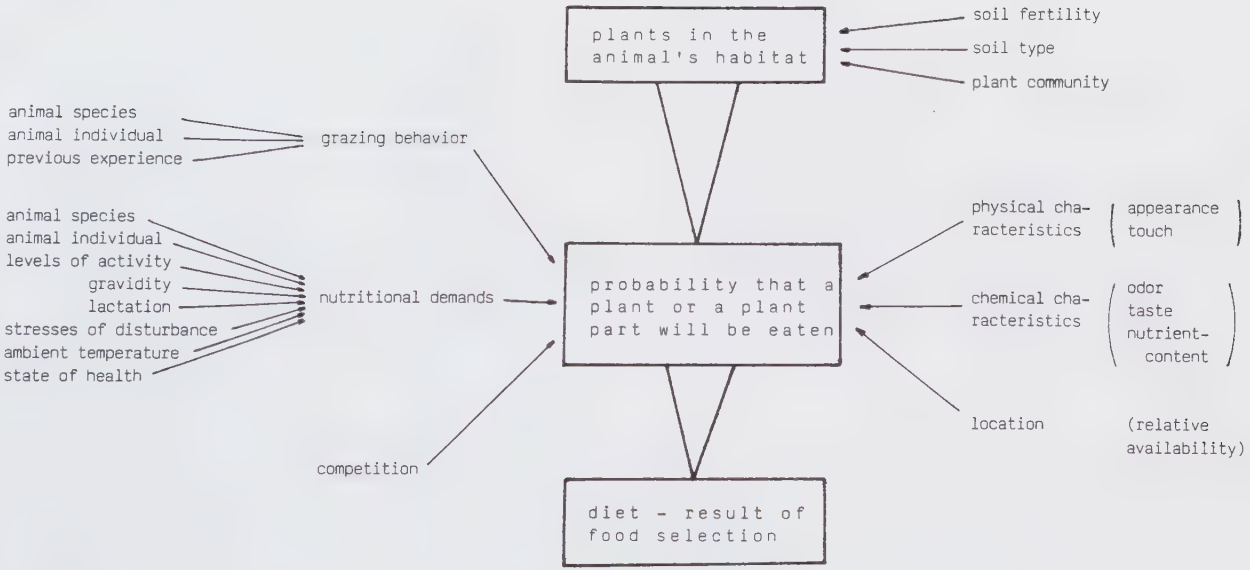

Fig.1: Variables determining food selection in ruminants.

senses. ARNOLD (1966a) showed for sheep that out of the five senses, vision plays a role in food search but not food selection *per se*. Touch, smell and taste, however, play major roles in the selection of food items. With sheep, each impairment of these senses caused a marked change in food selection, quantitatively and qualitatively (ARNOLD, 1966b), and these senses together determine food selection. Presumably in other ruminants too, a single sense will rarely be of paramount importance in food selection. This is adaptive in terms of reliability of the decision. Touch and smell will influence food selection before ingestion. Although ruminants can discriminate odors only at short distances (ARNOLD & HILL, 1972), they are able to discriminate exactly between adjacent plants and plant parts because of this. The last decision before swallowing is made by tasting the food.

Which characteristics of a food lead to its acceptance or rejection? What methods have been applied to determine this?

The hope of finding food characteristics - nutritive and/or non-nutritive - which generally influence food preference, has led to many investigations in this area. BELL (1959), GOATCHER & CHURCH (1970), CRAWFORD & CHURCH (1971), and RICE & CHURCH (1974) have studied the behavioral responses of ruminants to various chemicals by the "two choice" test method. In these tests, tap water was

offered together with a watery solution of the chemical to be tested. The intake of the solution in percentage of total fluid intake renders a measure of preference. Altering the concentration of the test solution results in a preference/concentration function. The data obtained in this way reveal that for all chemicals investigated, a zone of non-discrimination exists between solution and tap water, and all show a concentration beyond which rejection of the solution is more probable; however, total rejection of a solution never occurs.

These investigations are of somewhat limited value: Tests made in series with ascending concentrations yield different results than those with descending concentrations (KARE & FICKEN, 1963). Nor can the results be generalized for all ruminants, since there are great differences between species and even considerable ones within a species (ARNOLD & HILL, 1972). Additionally, these tests are made under rather unnatural conditions: 1) In the wild an animal is rarely confronted with a two choice situation, but rather with multiple choice situations; 2) Under natural conditions, the elements of choice are solids, not liquids; 3) The foods among which an animal normally has to select do not consist of a single chemical, but of a multitude of chemical components. And 4), because such components can interact with each other, the reaction of an animal to the simultaneous occurence of

several chemicals will not be the mere sum of the reactions to each component seperately.

Considering these drawbacks, other methods have been introduced. One is to determine the preference ranking of different food species. Following that the foods are analysed chemically. Then relationship between the amount of each chemical constituent and food preference is analysed. Using this approach, RADWAN & CROUCH (1974) analysed plant species of known preference by black-tailed deer (*Odocoileus hemionus*). No clear relationship to preference existed for any of the chemical constituents analysed. This is not surprising, since it is unlikely that selection is based only on a single constituent; it is more likely the result of a multifactorial decision.

A further method of estimation selectivity for nutrients in feeding is the "differential method": For this, part of a homogenous meadow is fenced off and grazed by a fistulated animal. Samples of the grazed herbage can be taken via the fistula and analysed. The differences between the grazed and non-grazed herbage indicate selectivity. HARDISON *et al.* (1954) conducted such investigations with cattle. They found that the grazed herbage had a greater proportion of protein and lower concentration of fiber than the original herbage. But did the animals actually select their foods on this basis,

or were the results simply a side-effect of selection occurring on another basis?

Still, the various results of analyses of ruminant food selection, regardless of methods utilized, can be summarized as follows: Nutritive properties which are potentially beneficial to the animal (sugars and soluble carbohydrates, proteins, fat, and vitamins) show either a positive or no relationship to preference; nutritive properties which could harm the animal or reduce digestibility (lignin, cell wall, crude fiber, tannins, toxins) show either a negative or no relationship to preference. This statement is generally accepted and is presumably valid for all ruminants (ARNOLD, 1964). More precise, generally valid statements cannot be made, because of the great variability between and within species, and the fact that variables such as environment, previous experiences and competition can alter food selection (ARNOLD, *op cit.*).

2.2 Nutritional requirements

It is difficult to sum up the nutritional requirements for ruminants in general, because they are indeed species-specific. Moreover, they are subject to various influences mentioned above and seen in Fig. 1.

For domestic animals, much literature on nutrient requirements does exist, including extensive reviews (e.g.

AGRIC. RES. COUNCIL, 1965; CHURCH, 1972). Much less data is available for wild ruminants (see BUBENIK, 1959; ABRAMS, 1968; WACKERNAGEL, 1966). The main reasons seem to be that wild ruminants are of little economical interest, and that there are simply so many different species. Because of different nutritional adaptations and different feeding aims in livestock and wild ruminants, data for livestock cannot be generalized to the latter. Thus, most recommended nutrient supplies for wild ruminants are deduced from the scant empirical data available. In spite of these difficulties, a few generally valid rules can be stated:

- The minimum metabolizable energy needed per kg metabolic weight per day is about 110 kcal (CHURCH, 1972; HELFERICH & GUETTE, 1972).
- Dry weight proportion of crude protein should not fall below 7% and should not exceed 20% per day (CHURCH, 1972; MENKE & HUSS, 1975).
- The diet should not contain more than 6% fat per day (CHURCH, 1972; HELFERICH & GUETTE, 1972).

2.3 Regulation of food intake

It is obvious that the amount of food ingested daily is limited. A pattern of duration of, and time intervals between feedings also exists, and these facts indicate that food intake is self-limiting. The responsible in-

hibitory stimuli are termed "inherent inhibitory stimuli" (McCLYMONT, 1967). Food intake regulation is necessary on the one hand to ensure that the gastrointestinal cavities not be overfilled (short-term regulation by hunger and satiety signals), and on the other hand, to maintain long-term energy balance (BAUMGARDT, 1970). But because a single meal contains a distinct amount of energy, short-term regulation of meal size and frequency is involved in long-term energy balance regulation. Energy balance is maintained either to keep the body weight of an adult at a constant level, or to control growth in the young BAUMGARDT, 1970; BAILE, 1971).

2.4 Diet optimization in wild ruminants

Although the regulation of food intake is fairly well understood, sections 2.1 and 2.2 indicated the paucity and confusion of background information on food selection and nutritional requirements in ruminants. From that information, it becomes clear that the controversy, over whether a wild ruminant is capable of selecting a "proper" diet, remains unsettled. GORDON & TRIBE (1951) demonstrated that at least two domestic ruminants, cattle and goats, were not able to select nutritionally optimal diets; but it is quite possible that these ruminants lost this capability during the process of domestication. On the other hand, ZAHORIK & HOUPT (1977)

proposed that free-ranging ruminants should be able to nourish themselves properly when in their ancestral habitat, because of a high adaptation to the foods presented there. But their model made no assumption of the ruminant's ability to select foods according to nutritive characteristics; this would be advantageous, even in the ancestral situation, if sudden changes in food availabilities occur.

In what follows, I have attemped to approach the questions of food selection and diet optimization in ruminants experimentally. The first-time application of linear programs to access possible nutritional "stratregies" proved to be interesting, and I regard the research presented here as a stepping-stone for further studies. Indeed, nutritional "strategies" were found, but I failed to demonstrate selection based upon nutritive characteristics of the food; non-nutritive properties (components) appeared to play a greater role in that selection.

3. Food-choice experiments with captive wild ruminants

3.1 Test animals

Principally, I had to choose between domestic and wild captive ruminants as test animals. The election of

domestic animals would have brought the advantage of much more available data on digestibilities of foods, useful in the interpretation of food-choice experiments. Using wild ruminants as test animals, few such data would be available and I would have to extrapolate from the data on domestic animals. Of course, this would cause some difficulties because of species-specific nutritional physiology. Nevertheless, it is very likely that certain capabilities in food selection and diet optimization have vanished during the domestication process (ARNOLD & HILL, 1972; BAILE & FORBES, 1974). Since these were the questions of major interest, I decided to risk working with captive, wild species.

Originally, I planned to work comparatively with two species of different feeding types, a concentrate selector and a grazer. After HOFMANN & STEWART (1972) and HOFMANN (1973), the ruminants can be divided into "bulk and roughage eaters"(=grazers), "selectors of juicy, concentrated herbage" (=concentrate selectors) and "intermediate feeders". These feeding-type classes are based upon differences and similarities in rumen morphology and digestive physiology, and I had reason to suspect that this might influence food selection capabilities. With this in mind, I sought out wild ruminants, kept under the following conditions:

- While eating, each animal should be kept in a separate stall.

- During the remaining time, the animals should be kept together in groups that would allow normal zoo social behavior.
- The enclosures and stalls should contain no supplemental food.
- For each species investigated, a minimum of four animals must be available, preferably of the same sex and the same age-class.

These conditions were met by the Arabian oryx (*Oryx leucoryx*) and the South African oryx (*Oryx beisa*) [see Plates 1 and 2] held in the Zoological Garden of Zurich, Switzerland. Unfortunately, both species are of the same

Plate 1: Female Arabian oryx with young.

feeding type - grazer - and very few data are available on their nutritional requirements. Although no additional food existed in the enclosures, straw beds in the stalls were unavoidable.

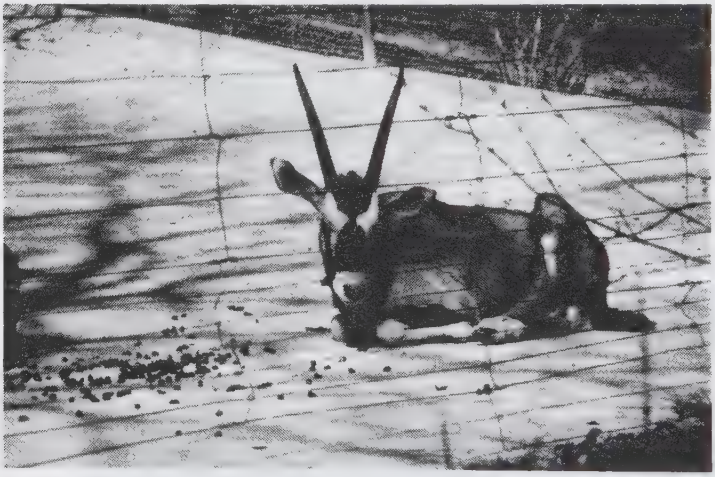

Plate 2: Young South African oryx.

Originally, the experiments were also performed on the greater kudu (*Tragelaphus strepsiceros*), a concentrate selector, but later on, my experiments had to be stopped, without a suitable replacement species being available, for the following reasons: First, the females and young are kept in a collective pen, where direct observation of individual feeding proved impossible. Secondly, these animals displayed enormous greediness, perhaps a result of the collective pen, and this greedi-

ness resulted in digestive problems (diarrhea) which would not disappear. After three weeks, the kudus had to be dropped from the program, and I was forced to continue with two, closely related species of the same feeding-type class.

Beginning in 1980, experiments were performed with four Arabian oryxes - two adult males, two adult females - and with four South African oryxes - one adult male, two adult females and one subadult male. In September 1980, the zoo acquired two additional adult Arabian oryx females, one of which arrived already pregnant. The successful breeding of the rare Arabian oryx - three females were born during my study - had the unfortunate side effect that food intake of a mother and its calf could not be separated until weaning. But at least mothers and calves were not placed all together in a collective pen. The experiments with the South African oryxes were somewhat less successful because one adult male ate so much that his digestion became impaired (although less severely than with the greater kudu), and because changes in the colony, due to proper animal management, reduced the periods of availability for certain animals. Essential data on all test animals utilized, appear in Table 1.

Spp.	Animal name + code number	Sex	Birth	Approx. Weight in 1980 (kg)	Kidding in 1980+1981	Data from --- to ---
Oryx leucoryx	Taif (2)		7. 4.74	50		29. 3.80 - 11.12.81
	Ramtha (3)		1. 3.78	60		29. 3.80 - 11.12.81
	Mukalla (1)		23. 7.77	50	3. 3.81	29. 3.80 - 2.12.81
	Madaba (4)		1. 2.78	50	11. 1.81	29. 3.80 - 2.12.81
	Amine (10)		26. 5.78	50	2.12.80	5. 9.80 - 2.12.81
	Sadafi (9)		25. 1.79	50	-	5. 9.80 - 2.12.81
Oryx beisa	Peter (7)		26. 7.70	170		17.11.80 - 6.11.81
	Zombo (8)		79	100		21. 7.80 - 28.12.80
	Susi (6)		7.11.64	150		6. 7.80 - 13. 5.81
	Kataba (5)		10. 7.70	150	14. 9.80	3. 5.80 - 2.12.81

Tab.1: Available data on the test animals.

3.2 Methods

3.2.1 Experimental design

The basic experimental method was that of multiple-choice experiments with *ad libitum* food supply. The use of two-choice experiments would have simplified interpretation of the results, but would have allowed the animals very

little freedom in mixing their own diets. Furthermore, a two-choice test only allows the comparison of one food property at a time. Because it is most likely that multiple factors simultaneously play a role in food selection, one would need a great number of different two-choice experiments in all combinations to assess which properties play a role in selection. The most natural experiment would be a multiple presentation of plants under controlled conditions; but in additions to the enormous expense of this, such an experiments would still contain too many uncontrollable variables. Therefore, the experiments were conducted with pelleted feeds. This provided several advantages: 1) Habituation time could be reduced by having the pellets made out of the same components used in the recipe for pellets fed the animals before my experiments. 2) I could vary the composition of the pellets, still using the same basic components, and hold that composition precisely constant throughout an experimental series. 3) Later, I could reduce the number of components to make analysis and interpretation simpler. And, 4) by omitting one or more of the pelleted feeds from the standard four-choice situation (i.e. four pellet-types, each made out of the same basic components, but in different proportions were usually offered), I could study an animal's reaction in food-choice.

To secure separate data from each animal, they were

housed in single stalls from 1800h to 0700h in summer, and from 1700h to 0800h in winter. Only during these periods, did they have access to the feeds.

As a concession to the zoo and the valuable animals, the Arabian oryxes recieved constant amounts of alfalfa hay, and the South African oryxes, meadow hay and carrots, daily and in addition to the pellets. The amounts of alfalfa or meadow hay and carrots offered were set to insure that these supplemental foods were completely ingested each day; 900gr of alfalfa hay for each Arabian oryx, and 2.5kg of meadow hay plus 1kg of carrots for each South African oryx, were presented.

The pelleted feeds were made up in such a way that no nutritional damage could occur, even if one food was eaten exclusively for a long period. This precaution was necessary, because I could not afford to loose an animal, either politically or from the standpoint of sample size. (Because the animals were receiving alfalfa hay or meadow hay daily, the pellets did contain less fiber than required as an exclusive food).

The components of the foods (pellets) and their ranges over all pellet types are listed in Table 2; detailed information is given in the Appendix, Table 15. A total of six experimental series were conducted between April 1980 and December 1981. The series were conducted chronologi-

Component	Series I	Series II	Series III	Series IV	Series V	Series VI
Barley	1.0 - 6.0	1.0 - 5.0	1.0 - 7.0	4.0 - 10.0	5.6 - 6.0	1.0 - 8.0
Corn	3.0 - 18.0	6.0 - 20.0	7.0 - 20.0	6.0 - 20.0	16.9 - 18.0	1.0 - 11.0
Rye	1.0 - 13.0	1.0 - 15.0	1.0 - 14.0	5.0 - 16.0	14.1 - 15.0	1.0 - 11.0
Soybean, solv-extd	0.5 - 20.0	0 - 16.0	0 - 20.0	0.5 - 20.0	3.8 - 4.0	1.9 - 7.0
Rape, solv-extd	0.5 - 10.0	0 - 8.0	0 - 9.0	0.5 - 12.0	1.9 - 2.0	4.8 - 5.0
Wheat, ground	0.5 - 4.0	0 - 3.0	2.0 - 3.0	4.0 - 6.0	5.6 - 6.0	1.9 - 15.0
Potato, ground	1.0 - 9.5	2.0 - 12.0	1.0 - 12.0	1.0 - 12.0	10.5 - 11.2	1.9 - 15.0
Straw, ground	-	-	0 - 4.0	2.0 - 16.0	3.8 - 7.8	2.8 - 27.6
Pomace	0.5 - 10.0	3.0 - 8.0	1.0 - 6.0	4.0 - 8.0	5.6 - 6.0	1.9 - 6.0
Mixed grass,ground	10.0 - 23.0	8.0 - 17.0	6.0 - 14.0	12.0 - 17.0	10.8 - 11.5	2.9 - 13.0
Molasses	3.0 - 4.0	2.0 - 4.0	2.0 - 5.0	2.0 - 5.0	3.8 - 4.0	2.9 - 3.0
Elements & vit.	8	8	8	8	7.5 - 8.0	8
Potato starch	-	-	-	-	0 - 4.0	22.5 - 36.3
Soybean protein	-	-	-	-	3.8 - 4.0	0 - 17.1
Chromium oxide	-	-	-	-	0.28- 0.3	0.17
Oats	1.0 - 6.0	1.0 - 4.0	2.0 - 5.0	-	-	-
Wheat	2.0 - 14.0	5.0 - 14.0	2.0 - 16.0	-	-	-
Linseed,solv-extd	0.5 - 10.0	0 - 7.0	0 - 9.0	-	-	-
Wheat bran	0.5 - 1.0	0 - 2.0	0 - 5.0	-	-	-
Rice, ground	0.5 - 2.0	0 - 2.0	0 - 5.0	-	-	-
Beet pulp	1.0 - 5.0	2.0 - 7.0	2.0 - 5.0	-	-	-
Coconut,solv-extd	1.0 - 15.0	1.0 - 14.0	1.0 - 12.0	-	-	-

Tab.2: Ranges of the food components within a food series (values in % of fresh weight). [For dates of each series, see Tab.15, Appendix].

cally, and between series, either the compositions of the pellets were altered, or one or more pellets types were eliminated (see also Fig. 2, p.33). Chromium oxide was added in Series V and VI, as a non-nutritious, external indicator used to determine digestibilities in faecal analyses.

For each pellet type in each food series, a proximate analysis was made. Additionally to crude fiber analyses, in Series IV ot VI, neutral detergent fiber analyses (NDF) were also performed for calculation of digestibility. Since, in these foods, a significant correlation exists between crude fiber and NDF ($z=2.618$; $\alpha \leq 0.01$), and for comparative purpose over all series, I have decided to use the values for crude fiber, instead of NDF.

In Table 3, minimum and maximum nutrient contents of the pellets in each food series are listed; detailed information on each pellet type can be taken from Table 16 in the Appendix.

It would be easier to interpret the aims of food selection from several different feed sets than only from one. This was accomplished by altering the four feeds in their percentages of nutrients; however, the components remained the same so as not to introduce new variables. Additionally, if during a series, it became evident that one food was strongly preferred over the others, this

Nutrient	Series I	Series II	Series III	Series IV	Series V	Series VI
Water	10.0 - 11.0	11.0 - 13.0	11.0 - 13.0	10.5 - 12.0	13.0	9.0 - 13.0
Protein	11.3 - 25.2	10.7 - 21.5	9.9 - 21.5	10.0 - 19.0	13.6 - 14.5	13.0 - 20.0
Fiber	7.6 - 13.1	7.3 - 12.6	7.0 - 12.3	8.7 - 13.6	7.8 - 8.7	7.8 - 12.7
NDF	-	-	-	15.0 - 23.1	13.3 - 15.9	14.6 - 21.5
Fat	2.7 - 3.7	2.1 - 2.8	2.1 - 3.2	2.0 - 3.3	1.8 - 2.0	0.8 - 2.3
Ash	5.7 - 6.9	8.3 - 9.2	8.1 - 8.4	9.1 - 10.9	8.5 - 9.2	8.7 - 9.2
NFE	43.6 - 59.9	45.1 - 57.8	46.0 - 58.9	45.9 - 56.9	52.8 - 54.7	51.2 - 54.7
Energy	3875 - 4075	3610 - 3840	3615 - 3875	3630 - 3735	3625 - 3640	3615 - 3845
Ca	0.44 - 0.80	1.08 - 1.26	1.04 - 1.18	1.02 - 1.14	0.96 - 1.06	0.79 - 1.01
P	0.53 - 0.79	0.87 - 0.90	0.77 - 0.82	0.74 - 0.87	0.64 - 0.78	0.64 - 0.75
NaCl	0.35 - 0.47	0.82 - 1.05	0.77 - 0.99	0.76 - 0.95	0.99 - 1.17	1.16 - 1.21

Tab.3: Ranges of the nutrient contents within a food series (values in % of fresh weight). [For dates of each series, see Tab.16, Appendix].

preferred food was omitted in the subsequent replicates of that series. By this means, the animals were forced to mix another diet from the remaining pellet types.

The schedule of the experiments is shown in Fig. 2, where one notes that neither the series, nor the durations of a series for individual animals, are of the same length. This was due to the fact that I could not predict total food consumption in advance of ordering the pellet batches; for economical reasons, I continued to use the pellets of a series until their supply was depleted.

Although it is well known that ruminants do not like "pure" foodstuffs, some single components of the pellets were offered to the animals during one experimental series (A in Fig. 2). I needed some indication of preference for the basic ingredients in the pellets, to later differentiate preferences for pellet type, nutrient content and components.

One last experiment was conducted to examine the effect of adding a secondary compound on food preferences (see Fig. 2). Pure tannin was chosen as test substance, and added to food IVD in ascending concentrations (0.1; 0.5; 1.0; 2.0 and 4.0% fresh weight) during successive replicates. Because the females were near term at this time, the test with 4% added tannin was only performed on the males. Along with the IVD-pellets containing tannin, an

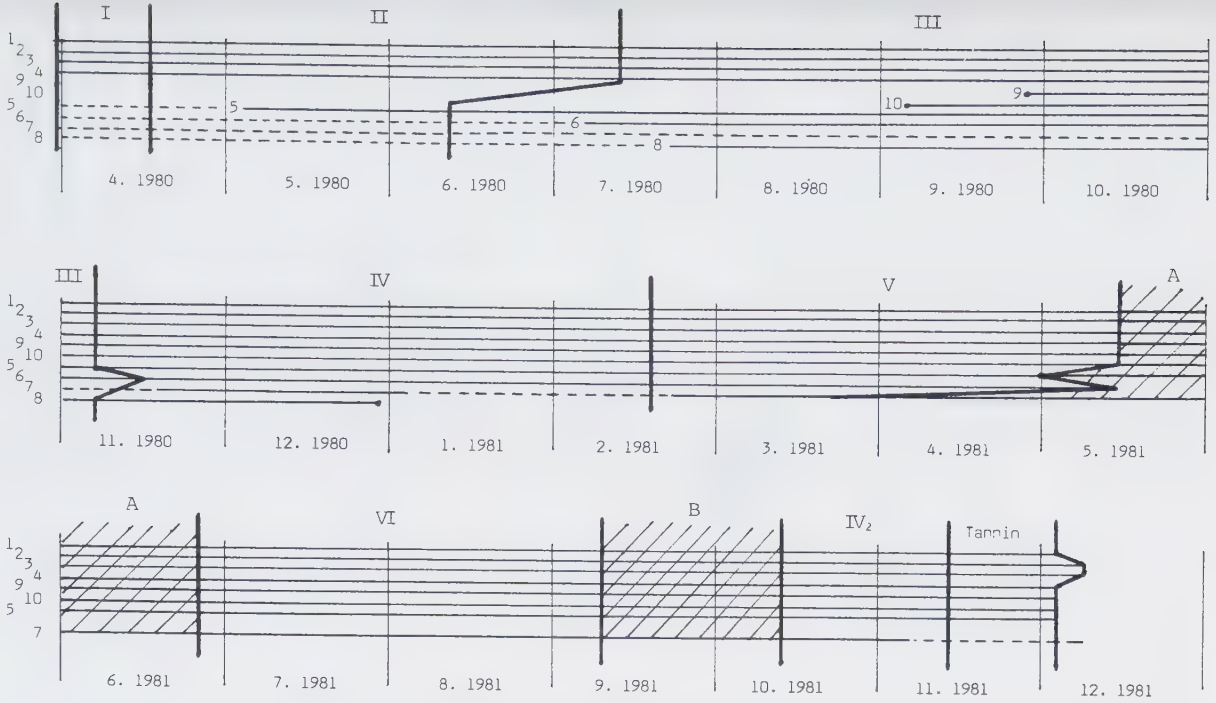

Fig.2: Schedule of the experiments.
Roman numbers I to VI: the different food series. (See Tabs.2 and 3).
Arabian numbers 1 to 4 and 9,10: the Arabian oryxes.
Arabian numbers 5 to 8: the South African oryxes.
"-------": Periods of no data collection for technical reasons.
A: Experiments with isolated food components.
B: No data collection, but continued feeding of experimental foods (Series VI). (Because of a course at Samburu Game reserve, Kenya).

alternative food was offered (food IVC), which had been less preferred than food IVD during Series IV, earlier.

3.2.2 Recording of the data

When the animals entered their stalls at 1800h, they were fed. The four pelleted foods were put in a frame in four identical dishes. The alfalfa hay for the Arabian oryxes was placed on the floor, (see Fig. 3), whereas the meadow hay for the South African oryxes was put into a wall rack.

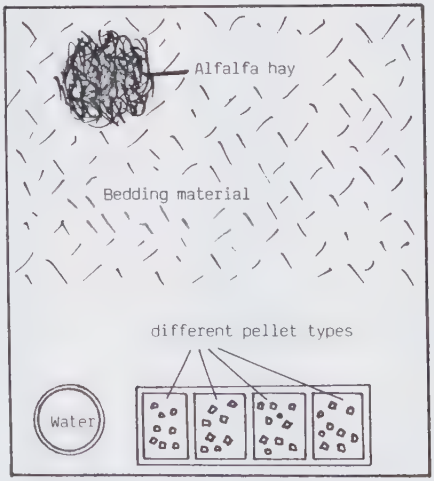

Fig.3: Arrangement of the different foods in the stalls.

To insure an *ad libitum* supply of pellets, they were presented in such quantities as to allow leftovers, even when an animal had fed only on one food.

At 0700h, the animals could leave their stalls, and the remaining food could be collected and weighed again. With this procedure, data on daily consumption of each

experimental food could be secured from each individual.

Direct observations revealed that the animals showed a position preference within the four dishes only when the frame was placed entirely to the edge of the stall. (Under these circumstances, the dish next to the edge was least preferred). As soon as the frame was placed 30cm or more away from the edge, as showing in Fig.3, all dishes were equally preferred. In spite of this, the four foods were filled at random into the four dishes each evening, to prevent the development of a position preference.

Whenever possible, direct observations were also made for qualitative notes on factors that might influence food consumption, e.g. onset and termination of female receptivity, unusual disturbances, etc.

3.2.3 Fecal analyses

To determine the digestibility of the feeds, two methods were employed: firstly, data from the existing literature were used to arrive at a mathematical estimate of this (after SALEWSKY, 1970). Secondly, samples of faeces from the previous night were collected from the individual stalls. Since it was not possible to collect faeces quantitatively, the inert, inabsorbable indicator, chromium oxide [Cr_2O_3], was added to all four feeds

during Series V and VI. During each of these series, and after completing data collection in the four-choice situation, each single pellet type was offered alternatively during a digestibility trial.

When one feeds chromium oxide during the first days of a series, a "pool" of Cr_2O_3 will establish itself in the stomach and during this, recovery rate in the faeces will be less than 100%. But after 7 to 10 days, one can assume that recovery rate will reach 100% for all additional Cr_2O_3 fed, as shown in experiments with cattle (WENK, pers.comm.).

Knowing the concentrations of chromium oxide in the food [c_F] and in the faeces [c_K], the concentration of a specific nutrient [N] in the food [n_F] and in the faeces [n_K] as well as the total amount of food eaten [F], one can estimate the digestibility of this nutrient [D_N].

The total amount of the nutrient N in the food is

$$N_F = F \cdot n_F$$

and the total amount of the nutrient in the faeces is

$$N_K = K \cdot n_K$$, whereby [K] is the total amount of faeces, here an unknown quantity.

the digestibility of the nutrient N is defined as

$$D_N = 1 - \frac{N_K}{N_F}$$, which can be rewritten as

$$D_N = 1 - \frac{K \cdot n_K}{F \cdot n_F}$$ (Equation I).

Because the rediscovery rate is 100%,

$$c_F \cdot F = c_K \cdot K \quad \text{or} \quad \frac{K}{F} = \frac{c_F}{c_K} \quad .$$

This equation, placed into equation I results in

$$D_N = 1 - \frac{c_F \cdot n_K}{c_K \cdot n_F} \quad , \text{ which can be solved.}$$

The concentrations of Cr_2O_3 applied were as follows: 0.28% in VA, 0.30% in VB, 0.29% in VC and D, and 0.17% in VI A through D. (The differences in the Cr_2O_3 -percentages are of no importance; I reduced the percentages in Series VI for economical reasons).

In a first step, I estimated the digestibility of organic matter [OM]. Should no significant differences in OM-digestibility of the feeds appear, then it is useless to examine the digestibilities of other nutrients (WENK, pers.comm.). To determine OM-digestibility, I used the standardized method of the Swiss Federal Institute of Technology (E.T.H. Zurich), where I performed the analyses. Their method shows only minor deviations from that described in NAUMANN & BASSLER (1976).

3.2.4 Analysis of data

In this study the raw data consist of the daily amounts of each food type eaten by an individual animal. For each food type the components and the results of the

proximate analysis are known. In a first step, the percent input of each pellet type is calculated, based on the total input of pellets. From this, pellet preferences can be recognized, assuming that preferences are proportional to relative intake. To facilitate the interpretation, these data were smoothed with a nonlinear data-smoothing algorithm, developed by TUKEY (1977), and programmed for computer by VELLEMANN & HOAGLIN (1981). The smoothing algorithm used is based on running medians, and is referred to in the literature as "4 2 5 3 H, twice". The smoothed data - pellet input - were then plotted against successive days, and diagrams were drawn by the Versaplot-07-system®. Results of the proximate analyses of the different feeds permited calculation of the total daily input of different nutrient classes (water, crude protein, crude fiber, crude fat, ash, nitrogen free extracts, sodium chloride, calcium, phosphorus, and gross energy). These data were also smoothed and plotted against successive days.

To determine whether one pellet type was significantly preferred over another, the mean intake of each pellet type was calculated. Because food preferences are unstable at the beginning of a test series and later stabilized, only data from the stabilized period were used in calculation of mean food intakes. To define "stabilized" food selection, the one food which contri-

buted at least 85% to total pellet intake was considered. (If no one food was preferred to such an extent, the second, or the second and third preferred food were also considered). If the percent intake of this food differs at an arbitrary day by not more than ±5% from the percent intake on the following day, and this condition holds for at least seven days, food selection was said to be stable. Additionally, the coefficient of variability after Pearson (WEBER, 1972) had to be ≤5.0 during the stabilized period.

By arranging the different food types according to decreasing intake, for each animal and for each food series a preference order resulted. These preference orders were tested for significance at α=0.05 with Duncan's new multiple-range test (WEBER, 1972).

Early on, it appeared as though different individuals showed the same preference ranking of the four pellet types, which might imply generalized preferences. To test this, the foods were ranked according to the animal's preference, and for each series the data from all animals were pooled. Duncan's new multiple-range tests were conducted to determine any generalized preference orders. Significant, generalized orders were found (see Tab.6, p.53), but they were not the same in all food series.

Should significant preference orders among food types

exist, then selection would have to have been based upon differences in the amounts of either the nutrients, or the more holistic components (e.g. barley) of those foods. All other attributes, such as shape and color of the pellets were held constant.

One method of recognizing which food properties are important in food selection is to test all properties for their correlation with preference. But because autocorrelations between different food properties can mask correlations between a specific food property and food preference, it is first necessary to examine the food properties themselves for autocorrelations. Only those food characteristics that showed significant correlations with preference were examined for autocorrelations, using the Kendall correlation coefficient τ.

The tests for correlations between preference and properties of a food were performed as follows: In a first step the preference orders among the four pellet types were split into pairs with decending preference. (e.g. A>B>C≈D was split into A>B, A>C, A>D, B>C, and B>D; or A≈B>C≈D, into A>C, A>D, B>C, and B>D). Following that, all pairs of a food series were pooled. Using the Wilcoxon matched-pairs signed-ranks test (SIEGEL, 1958), I determined whether food characteristics occurred in a similar concentration, both in the preferred- and in the less-preferred foods, or whether a significant difference

existed between these two classes. The Z-values of the Wilcoxon test are a measure of the "distance" from equality between the matched pairs (SIEGEL, 1958), whereas at equality, the Z-value is zero. For my purposes, the Z-values serve as a measure of the importance of a food characteristics in food selection. A quality which is significantly correlated with preference (high Z-value) contributes more to food selection than another food quality, which is not significantly correlated with preference (low Z-value).

3.2.5 Computer simulation of food selection

WESTOBY (1974) had suggested the use of linear programs for determining optimal diets, and such a linear program is shown in Tab.4. He suggested that energy maximization

Character	$Food_1$	$Food_2$	$Food_3$	$Food_j$	Constraint	Right-hand side
1) % fibre	$a_{1,1}x_1+$	$a_{1,2}x_2+$	$a_{1,3}x_3+$	$a_{1,j}x_j$	$\geq$	20.0 %
2) % fat	$a_{2,1}x_1+$	$a_{2,2}x_2+$	$a_{2,3}x_3+$	$a_{2,j}x_j$	$\leq$	6.0 %
3) % protein	$a_{3,1}x_1+$	$a_{3,2}x_2+$	$a_{3,3}x_3+$	$a_{3,j}x_j$	$\geq$	13.0 %
i) kcal Energy	$a_{i,1}x_1+$	$a_{i,2}x_2+$	$a_{i,3}x_3+$	$a_{i,j}x_j$	=	Maximum (objective function)

Tab.4: Principe of linear programms for calculation of optimal diets (after WESTOBY, 1974). In this example energy is maximized under the above constraints.

might be an appropriate objective function. But it is

also possible that other objective functions may play a role, especially if gross energy content of the different foods does not vary greatly , as in my experiments (see Tab.3, p.31).

The solutions of these linear programs would be diets which fulfil the nutrient constraints (the inequalities in Tab.4) and one objective function (the equality). As mentioned in the introduction, the problem is determining the constraints operating upon the animal. There are three levels of nutrient constraints: The least restrictive constraints are the physiological ones. If an attribute of a diet falls outside of such a constraint, illness will result whenever that same diet is consumed in the same quantity over a longer period. The most restrictive constraints would be those, resulting in the optimal diet (optimum constraints). A third level, the "inherent constraints", is found between the two extremes. By definition, these constraints come into action in the animal's food selection, and they must exist if food selection is even partly based upon nutrient content. If an animal were to search for and combine foods using "optimum constraints", it would rarely secure such a diet. Use of "physiological constraints" would be disadvantageous, in that the resulting diet(s) would be least beneficial for the animal. In other words, any constraint lying inside the "physiological constraints" would be of

beneficial use to the animal. Therefore, we need to know the values of the "inherent constraints" to construct the above-mentioned linear program. But these data are also not available!

Given the preceding argumentation, any constraint-value 'inside' the "physiological constraints" will suffice to guarantee the animal's nutritional health. And, the closer a hypothetical constraint lies to the "optimum constraint", the lower the probability of securing a diet fulfilling all constraints. Therefore, it would be best to propose hypothetical constraints, which lie between the inherent and the physiological constraints, naturally closest to the inherent constraints. Such constraints were established in the following manner:

1. The mean total food intake was calculated from the experimental data.
2. For each set of four pelleted foods, that food was determined which had a) the highest energy content, b) the highest protein content, c) the highest content of NFE [nitrogen free extracts], and/or d) the lowest fiber content.
3. For each of these foods the concomitant intake of the various nutrients was calculated, assuming an animal would eat the total mean amount of just that food.
4. The highest and lowest values found were taken as the hypothetical, nutrient constraints.

This method was applied for both the Arabian and the South African oryxes, naturally using the corresponding values, where species-dependent.

If the diet observed in the feeding experiments is really dependant on nutrient constraints, one should be able to establish an association between the observed diet and a diet, computed with the use of suitable, artificial constraints and different objective functions. Of course, this is only true, if one of the objective functions tested represents the "strategy" of an animal.

Linear programming was completed using subroutine ZX3LP in the IMSL library (see e.g., STIEFEL, 1965). The following objective functions were set:gross energy maximum, crude protein maximum, NFE maximum and fiber minimum. These objective functions were applied to diets of the Arabian oryxes consisting of 1)alfalfa hay and four pellet sorts of a series, or 2) alfalfa hay and three pellet sorts, (the most preferred pellet is omitted). For the South African oryxes the objective functions were applied to diets consisting of 1) meadow hay, carrots and all four pellets sorts, or 2) meadow hay, carrots and three pellet sorts.

Results were obtained on two levels: a) the optimal diet, given in amounts of the four, or three pelleted foods, respectively, and b) the amount of different

nutrients which would be ingested given this diet. These data sets were then compared with the observed data obtained in the experiments. For this, a measure of distance was needed. I could not use the "generalized distance" method of Mahalanobis (WEBER, 1972), since I was comparing data from samples with theoretical values. instead, the following procedure was applied: For each animal and for each data period within a series (periods, during which the foods offered remained constant), those segments were selected where food choice was stable (see pp.38/39). During the adaptation period when the animal is stabilizing its diet, no strategy of selection should be detectable. From these selected data periods, the arithmetical mean amounts of ingested nutrients, in % of total intake, were calculated. (If sample size is large enough, the arithmetical means are more relevant to the animal than its temporal function, for physiological reasons). For calculation, a minimum sample size of 10 successive days was required.

These mean values were then compared with the theoretical values: The differences between theoretical values and mean values were calculated for each of the food characteristics crude protein, crude fiber, NFE, and gross energy. The sum of the absolute differences for fiber, protein and NFE served as a measure of distance between the real and theoretical diets. (The difference for gross energy could not be used because of its different unit

of measurement). One obtains four distance values with this method - one for each of the four objective functions maximum protein intake, maximum NFE intake, maximum energy intake, and minimum fiber intake - and those for each animal and each test period. By definition, the one comparison with the smallest sum of differences corresponds to the most probable strategy the animal used in that test period.

3.3 Results

Before presenting the results, a word on omission of raw data in the dissertation itself is called for. The analysis of the data, particularly concerning graphical plottings of pellet and nutrient intake (smoothed values), produced reams of computer printouts. It would be neither useful (because of repetitions), nor practical (because of page limitaitons), to include these data in the dissertation or even an attached appendix. The data shown are sufficient to verify all interpretations, and should be considered as examples of the point in question. Only data which are redundant, have been omitted. My dissertation adviser (and director of the research project) has examined the original printout, now stored in the archives of the department, Ethology and Wildlife Research, of the Zoology Institute. Should it be deemed necessary, arrangements may be made to view these data

by appointment with the department.

To assist the reader and facilitate visual comparison of data from different animals and/or food series, all figures presented in the first section (plots of pellet intake) have been placed together at the rear of section 3.3.1 in chronological order. As an example of the raw data treatment, corresponding cuts of the raw data, the percentual contribution of the four pelleted foods, and smoothed values are shown in Tab.17 and Fig.18 of the Appendix. The total daily input of the different nutrients and their smoothed values are then shown in Tab.18 and Fig.19.

3.3.1 Food preferences

Initially, the pellets were preferred over the supplemental food (hay) by all animals, as indicated by consumption of the pellets first and hay later. Nevertheless, the hay was always totally consumed. After a year of continuous experiments, the Arabian oryxes (as opposed to the South African oryxes) began eating the alfalfa hay prior to the pellets.

Olfactorial examination of the pellets was usually very short - on the order of about one or two seconds. Whenever a new set of pelleted foods was offered, this increased in intensity and usually all different foods

were examined before one food was picked. Examination by taste was hardly ever seen, but during the first five to ten days after introduction of a new food set, total food intake was less than normal. During this period, changes in preference were frequent, and normally pellets of all four or three types were consumed.

The duration of this introduction period was neither typical for an individual, nor for a food set (series). For example in experiment III A-D, food selection did not stabilized for animal Nr.1 until 14 days, end even then pellets A and D competed wich each other for highest preference. On the other hand, the diet of animal Nr.2 in the same series stabilized after six days (see Figs. 5a and b, pp.67 and 68). Only in food series VI was the introduction period generally short (see Figs.9a-g, pp. 91-97). In this food series, preferences are quite clear and almost identical for all animals; animal Nr.5 (Fig. 9g) is the only exception. This may indicate less difficulty in decision-making during this series.

After the introduction period, the preferences stabilized and in most cases, did not alter thereafter (Tab.5; see also e.g. Fig.7a, p.77).

When comparing the preference orders of different animals in Tab.5, it is obvious that individual differences are small relative to similarities between animals. The

a)

Animal 1 ♀		Animal 3 ♂	
Food series	Preference order	Food series	Preference order
I A-D	A > B > C ≈ D		
II A-D	A >> B ≈ C ≈ D	II A-D	A >> C ≈ B ≈ D
II B-D	D > C > B	II B-D	C ≈ D > B
III A-D	A > D > C ≈ B	III A-D	A >> B ≈ C ≈ D
III B-D	D >> C ≈ B	III B-D	B >> D ≈ C
IV A-D	B >> A ≈ C ≈ D	IV A-D	A > B > D ≈ C
V A-D	C > B > D ≈ A	V A-D	C > D > B ≈ A
VI A-D	A >> B ≈ C ≈ D	VI A-D	A >> B ≈ C ≈ D
VI B-D	C >> B > D	VI B-D	C > B > D
Animal 2 ♂		**Animal 4 ♀**	
I A-D	B > A > C ≈ D		
II A-D	A > D > C > B	II A-D	A >> B ≈ C ≈ D
	[D > A >> B ≈ C]		
II B-D	D >> B ≈ C	II B-D	B > D > C
III A-D	A >> B ≈ C ≈ D	III A-D	A >> B ≈ C ≈ D
III B-D	B >> C ≈ D	III B-D	B > C ≈ D
IV A-D	B >> A ≈ C ≈ D	IV A-D	D >> B ≈ C ≈ A
	[D >> B > C ≈ A]		
V A-D	B > C > A ≈ D	V A-D	C ≈ A > B ≈ D
VI A-D	A >> B ≈ C ≈ D	VI A-D	A >> B ≈ C ≈ D
VI B-D	C >> B ≈ D	VI B-D	C >> B ≈ D
Animal 9 ♀		**Animal 10 ♀**	
III B-D	B >> D ≈ C	III B-D	C >> B ≈ D
IV A-D	B > A > D > C	IV A-D	A >> B ≈ C ≈ D
			[B >> A ≈ C ≈ D]
V A-D	B ≈ C > A ≈ D	V A-D	C ≈ B ≈ A > D
VI A-D	A >> B ≈ C ≈ D	VI A-D	A >> B ≈ C ≈ D
VI B-D	C >> B ≈ D	VI B-D	C > B > D

Tab.5: Preference orders among pelleted foods by a) Arabian oryxes and b) South African oryxes
>>: highly significant difference in preference (α≦0.01)
>: significant difference in preference (α≦0.05)
≈: no significant difference in preference
[ ]: preference order after a switch in preference

Animal 5 ♀		Animal 7 ♂	
Food series	Preference order	Food series	Preference order
II A-D	A > B > D > C		
III A-D	A ≈ B >> C ≈ D		
III B-D	B > D ≈ C		
IV A-D	B >> A > D ≈ C	IV A-D	A ≈ B >> C ≈ D
V A-D	C > B ≈ A > D		
VI A-D	D > A > C ≈ B	VI A-D	A > C ≈ B > D
VI A-C	A > C > B		[A >> C ≈ B ≈ D]
Animal 6 ♀		**Animal 8 ♂**	
III A-D	A > B > C ≈ D	III A-D	A > B > C ≈ D
III B-D	B >> C ≈ D	III B-D	B > D > C
IV A-D	A > B > C ≈ D	IV A-D	A > B > D ≈ C
V A-D	C > B > A ≈ D		

Tab.5b

greatest conformity exists among the animal's choice of most preferred food in a series. Lack of significant preference between two foods ("≈", in Tab.5) may be due to two causes: 1) The two foods may have competed with each other, alternating in rank over time, or 2), the intake of both foods may have been too similar. A good example of both is given in Fig.5e (p.71). (Two food types, x and

y, were said to compete with each other in an otherwise stabilized food selection, whenever neither of those foods alone fulfilled the criteria for stabilized food selection (see pp.38/39), but did so if the sum of x and y was considered).

The rare switches in food preference after the adaptation period (see Tab.5) were of two sorts: 1. The preference ranks broke down for a few days, but were re-established more or less in the same way later in the series (e.g. Fig.7e, p.81). or 2., the first ranking order broke down and a new order was established (e.g. Fig.6a, p.73).

Looking more closely at the most preferred pellet type of the different animals in each series, one notes high agreement between the animals in Series II, III and IV; for Series I, too few data are available to judge consistency of preference. In Series IV, pellets A and B appear to compete (but not by definition!) for first ranking, as do pellets B and C in Series V. In spite of very small differences in concentrations of components and nutrients in Series V (see Tabs.15b and 16b in the Appendix), which is probably the reason for different first-rankings, the preference orders were astonishingly clear and stable within each animal (see Figs.4-9, pp.62-97).

From all data on pellet selection in all series (see

examples of these data in Figs.4-9, pp.62-97), the following generalizations can be made:

- For food selection to stabilize up to 14 days were required ($\bar{x}$ = 4d).
- Except for Series V, where the different foods were quite similar, a clear separation between preferred and "refused" foods always became evident.
- One or two foods were always highly preferred over the others, and accounted for 85 or more percent of the total pellet intake.
- The majority of the animals preferred the same food type.
- Though the less preferred foods only made up at most 20% of the diet, it was rare that they remained untouched.

Although similarities in food selection between the different animals were evident, statistical tests revealed that only in Series I, III and VI were generally valid food preferences to be found (Tab.6). This implies that along with food characteristics of general importance in food selection, there may also be other cues, whose importance varies from animal to animal. To assess these, the correlations between food preference and food characteristics, calculated from the preferences of each animal (Tab.7), were compared with those, calculated

from the preferences of all animals in the pooled Series I, III and VI (Tab.8).

Food series	Preference order	
I	A ≈ B > C ≈ D	*
II	A > D > B ≈ C	
III	A > B > D ≈ C	*
IV	B > A > D ≈ C	
V	C > B > A ≈ D	
VI	A > C > B ≈ D	*

Tab.6: Generally valid preference orders. "" indicates significance of the preference order at α=0.05. (See Text, p.39).*

Visual comparison indicates similar Z-values for a characteristic between animals (Tab. 7), and significant relationships between food characteristics and generalized preferences (Tab.8). Because of different animals, the Z-values themselves cannot be compared mathematically. Thus, the criteria "significant correlation" and "non-significant correlation" (at $\alpha = 0.05$) are used for comparisons. Since the correlations for the different animals between preferences and food characteristics are not contradictory, the pooled correlations are assumed to represent general valid correlations.

It can be concluded that cereals, potato and NFE content are generally higher in the preferred foods and consistently preferred among all animals (Tab.7). Looking across the animals in Tab.7, the preferences for molasses, pomace and water are less consistent. Most animals did

Food character	Z-values and direction of correlation for each animal								
	1	2	3	4	9	10	5	6	8
Cereals	+ 3.12	+ 3.07	+ 3.34	+ 3.16	+ 2.80	+ 2.83	+ 2.77	+ 2.86	+ 2.80
Soybean,solv-extd	- 2.01	- 2.50	- 2.79	(-)1.90	--	(-)1.54	- 3.42	- 2.80	- 2.80
Rape, solv-extd	(-)1.62	- 2.21	- 2.93	- 2.39	--	--	- 3.21	- 2.80	- 2.85
Wheat, ground	(-)1.11		(-)1.40		+ 2.52	+ 2.67			
Potato	+ 2.22	+ 2.93	+ 2.72	+ 3.18	+ 2.37	+ 2.60	+ 2.33	+ 2.40	+ 2.40
Straw	- 3.00	- 2.77	(-)1.03	- 2.31	- 2.93	(-)1.44	(-)0.72	(+)0.22	(+)0.92
Pomace	+ 2.54	+ 1.98	+ 2.64	+ 2.56	--	+ 2.43	(+)1.84	--	--
Grass	(-)0.75		(-)0.19				(-)2.09		
Molasses	+ 2.95	+ 3.30	(+)1.87	+ 2.04	--	--	+ 2.12	(+)0.28	(+)0.28
Water	+ 2.36	+ 2.73	+ 2.90	+ 2.69	--	(+)1.01	0.03	--	--
Crude protein	- 2.05	- 2.37	- 2.87	- 2.42	(-)1.61	- 2.43	- 2.61	- 2.80	- 2.80
Crude fiber	- 2.58	- 3.42	(-)1.64	- 3.40	- 2.67	(-)1.19	- 3.32	(-)1.06	(-)1.07
Fat	(+)0.30	(+)0.30	(+)0.56	(+)0.56	--	--	(-)1.12	--	--
Ash	- 1.96	- 1.96	--	--	--	--	--	--	--
NFE	+ 2.53	+ 2.81	+ 2.96	+ 3.30	+ 2.49	+ 2.41	+ 3.99	+ 2.62	+ 2.43
Energy	- 2.29	- 3.20	- 2.66	- 2.90	--	--	- 2.27	--	--
NaCl	(-)1.35	(-)1.18	- 2.53	- 2.46	--	--	- 2.20	- 2.35	- 2.52
Ca/P	(+)0.71	0.02	(+)1.72	(+)0.88	(+)0.89	(+)1.68	(+)1.04	0.40	0.56
Fiber/NFE	- 3.11	- 3.85	- 2.86	- 3.76	- 3.06	- 2.02	- 3.91	- 2.23	(-)1.68

Tab.7: Correlations between food preference and food characteristics, calculated for each animal from the preference orders in all food series. The numbers are the z-values from the Wilcoxon matched-pairs signed-ranks test. Signs indicate the direction of the correlation. Signs in parentheses indicate non-significant correlations. For α=0.05, $z \geq 2.18$ (one-tailed test), or ≥ 2.44 (two-tailed test). "--" means that this food characteristic occurs in all four foods at the same concentration.

avoid soybean- and rape solvent-extracted, high protein-, fiber-, NaCl- and gross energy content. With one exception, fiber:NFE ratio was lower in the preferred foods.

Character	Z-value	Character	Z-value
Cereals	+ 3.18	Water	+ 2.52
Soybean,solv-extd	- 2.49	Crude protein	- 3.04
Rape, solv-extd	- 2.67	Crude fiber	- 2.97
Wheat, ground	(-)1.15	Fat	--
Potato, ground	+ 2.98	Ash	--
Straw, ground	(-)0.13	NFE	+ 3.20
Pomace	(+)1.73	Gross energy	- 3.06
Mixed grass,ground	0.10	NaCl	(-)2.14
Molasses	- 2.20	Ca/P	(-)1.60
		Fiber/NFE	- 3.20

Tab.8: Correlation between food preference and food characteristics, calculated from the generally valid food preference orders in the Series I, III, and VI, as listed in Tab.6.
The numbers are the z-values from the Wilcoxon matched-pairs signed-ranks test. Signs indicate the direction of the correlation. Signs in parentheses indicate non-significant correlations. For $\alpha=0.05$, $z \geq 2.18$ (one-tailed test), or ≥ 2.44 (two-tailed test). "--" means that this food characteristic occurs in all four foods at the same concentration.

It may seem surprising that high protein- and energy content are avoided. But with respect to protein content, the observed food selection results in an ideal percentual protein intake (see also Fig.15c, p.111), given that the

animals are grazers and not concentrate selectors. (A preference for the high-protein foods would have resulted in too high a protein intake).

The energy content within a food series did not vary greatly (ν = 3.0 or less), and therefore, the motivation to choose that food with the highest energy content was probably low. More importantly, the variation in NFE content within a food series was much higher (ν = 12.0 or more), and a high NFE content is strongly preferred. Since a strong negative correlation between NFE- and energy content exists (τ = -0.454; Z = 3.11, Kendall correlation coefficient), I suspect that a lower energy content is not really preferred by the animals, but rather the result of the animal's preference for NFE-rich foods.

Some animals (Nrs.1, 2, 4 and 9) significantly avoided foods with high straw content, others did not. On the other hand, all animals always completely consumed their hay ration, which was very high in fiber. The need for fibrous substances for a proper digestion is well known (CHURCH, 1972).

In Tab.9 the correlations are presented by food series. Only a few correlations diverge from expectation, i.e. differ from the generally valid correlations in Tab.8. In some cases these discrepances can be explained by the existence of autocorrelations between the food charac-

Character	Food series I	II	III	IV	V	VI
Cereals	+ 2.67	+ 2.75	+ 5.06	+ 4.09	1.69	+ 3.67
Soybean, solv-extd	- 2.67	- 2.44	- 4.70	- 3.45	-	0.96
Rape, solv-extd	- 2.67	- 2.38	- 4.70	- 4.33	-	-
Wheat, ground	0.85	- 3.37	1.01	+ 2.44	-	+ 4.68
Potato, ground	+ 2.55	0.99	+ 4.05	+ 4.78	-	+ 3.96
Straw, ground	-	-	+ 3.37	- 3.08	- 4.13	- 4.37
Pomace	1.86	+ 2.77	0.96	+ 3.81	-	+ 3.96
Mixed Grass, ground	1.84	- 3.51	- 3.41	- 4.45	-	- 4.68
Molasses	1.83	+ 3.28	+ 4.54	+ 2.16	-	-
Potato-starch	-	-	-	-	+ 3.06	- 2.60
Soybean-protein	-	-	-	-	-	- 4.28

Tab.9: Correlations between food preference and food characteristics, calculated for each food series from the preference orders of all animals. The numbers are the z-values from the Wilcoxon matched-pairs signed-ranks test. Signs indicate the direction of the correlation. At $\alpha=0.05$, correlation is significant if $z \geq 2.18$ for a one-tailed test, or $z \geq 2.44$ for a two-tailed test. "-" means that this food characteristic occurs for all four foods in the same concentration.

Character	Food series					
	I	II	III	IV	V	VI
Water	1.83	+ 2.20	+ 3.41	- 3.87	-	+ 3.67
Crude protein	- 2.67	- 2.49	- 4.50	- 3.55	-	- 2.60
Crude fiber	- 2.43	- 2.38	- 4.19	- 2.89	- 3.02	- 3.73
Fat	-	1.41	- 4.20	-	-	+ 3.63
Ash	- 2.52	0.24	-	1.80	-	-
NFE	+ 2.67	+ 2.38	+ 4.66	+ 4.45	+ 3.11	+ 3.70
Gross energy	- 2.52	- 3.05	- 4.20	0.87	-	- 3.91
NaCl	1.83	- 3.43	- 4.78	0.87	0.06	-
Ca/P	1.84	+ 3.84	1.01	+ 2.15	0.71	+ 3.81
Fiber/NFE	- 2.43	- 2.72	- 4.52	- 4.23	- 4.06	- 4.15
Protein/fiber	1.36	0.67	- 2.85	1.31	- 3.72	0.66

Tab.9 (cont'd).

teristics, presented in Tab.10. Thus, the unexpected positive correlation between straw content and preference in Series III is likely to be due to the positive autocorrelation with potato (a preferred component) in Series III. Likewise, the negative correlation between fat and preference in Series III (Tab.9) can be explained by the negative correlation with straw (Tab.10), which in turn, is positively correlated with potato in that series. (Fat content was not related to general preferences and occurred in all foods at the same concentration). However, not all discrepances can be explained in this manner. For example, a negative correlation between water and preference appeared in Series IV and no significant autocorrelations were found between water content and other characteristics during this series.

The autocorrelations between food components and nutrients in Tab.10 are of special interest, because they might offer hints on whether preference for a nutrient was real, or simply feigned by an autocorrelation with a preferred food component. Looking across all food series in that table, positive correlations were found between the following nutrient/component characteristics: protein/soybean solv-extd, protein/rape solv-extd, Fiber/straw, NFE/cereals, NFE/potato, and energy/soybean solv-extd. Unfortunately, all of these food characteristics were also singularly correlated with preference, and the

Pairs of character	Food series						
	I	II	III	IV	V	VI	(I-VI)
Water / fat	0	0	0	0	0	+	0
Water / molasses	0	0	+	0	0	0	0
Water / grass	0	0	-	0	0	0	0
Protein / cereals	-	0	0	0	0	0	0
Protein / soybean, solv-extd	+	+	+	+	0	0	+
Protein / rape, solv-extd ..	+	+	+	0	0	0	+
Protein / energy	0	0	+	0	0	+	+
Protein / NFE	-	0	-	0	0	0	-
Fiber / molasses	0	0	-	0	0	0	0
Fiber / straw	Ø	Ø	0	0	+	0	+
Fat / water	0	0	0	0	0	+	0
Fat / straw	Ø	Ø	-	0	0	0	0
NFE / cereals	+	+	0	+	0	0	+
NFE / soybean, solv-extd ...	0	0	-	0	0	0	0
NFE / grass	0	0	0	-	0	0	0
NFE / potato	0	0	0	0	0	0	+
NFE / rape, solv-extd	0	0	-	0	0	0	0
NFE / starch	Ø	Ø	Ø	Ø	+	0	0
NFE / protein	-	0	-	0	0	0	-
NFE / energy	0	0	-	0	0	0	-
Energy / cereals	0	-	0	0	0	0	0
Energy / soybean, solv-extd	0	0	0	+	0	0	+
Energy / protein	0	0	+	+	0	0	+
Energy / NFE	0	0	-	0	0	0	-
Cereals / Soybean, solv-extd	-	0	0	0	0	0	0
Cereals / rape, solv-extd ..	-	-	0	0	0	-	-
Cereals / Wheat, ground	0	0	0	0	0	+	0
Cereals / potato	0	0	0	0	0	+	0
Cereals / straw	Ø	Ø	0	0	0	-	0
Cereals / pomace	0	0	0	0	0	+	0
Cereals / starch	Ø	Ø	Ø	Ø	0	-	0
Cereals / NFE	+	+	0	+	0	0	+
Cereals / protein	-	0	0	0	0	0	0
Soybean, solv-extd / cereals	-	0	0	0	0	0	0
Soybean, solv. / rape, solv.	+	+	+	0	+	0	+
Soybean, solv-extd / protein	+	+	+	+	0	0	+
Soybean, solv-extd / NFE ...	0	0	-	0	0	0	0
Rape, solv-extd / cereals ..	-	-	0	0	0	-	-
Rape, solv. / soybean, solv.	+	+	+	0	+	0	+
Rape, solv-extd / protein ..	+	+	+	0	0	0	+
Rape, solv-extd / NFE	0	0	-	0	0	0	0

Tab.10: Autocorrelation between the different food characteristics.
+: significant positive correlation
-: significant negative correlation
0: no significant correlation
Ø: no test possible, because of absence of one food characteristic.

Pairs of character	Food series						
	I	II	III	IV	V	VI	(I-VI)
Wheat, ground / cereals	0	0	0	0	0	+	0
Wheat, ground / straw	Ø	Ø	0	0	0	-	0
Wheat, ground / pomace	-	0	0	0	0	-	0
Wheat, ground / starch	Ø	Ø	Ø	Ø	0	-	0
Wheat, ground / soybean prot.	Ø	Ø	Ø	Ø	+	-	0
Wheat, ground / grass	0	0	0	0	0	+	0
Potato / cereals	0	0	0	0	0	+	0
Potato / straw	Ø	Ø	+	0	0	0	0
Potato / wheat, ground	0	0	0	0	0	+	0
Potato / grass	0	0	0	0	0	+	0
Potato / starch	Ø	Ø	Ø	Ø	0	-	0
Potato / soybean protein	Ø	Ø	Ø	Ø	+	+	+
Straw / cereals	Ø	Ø	0	0	0	-	0
Straw / potato	Ø	Ø	+	0	0	0	0
Straw / wheat, ground	Ø	Ø	0	0	0	-	
Straw / fat	Ø	Ø	-	0	0	0	0
Straw / fiber	Ø	Ø	0	0	+	0	+
Pomace / cereals	0	0	0	0	0	+	0
Pomace / wheat, ground	-	0	0	0	0	-	0
Pomace / grass	0	0	0	0	+	0	0
Pomace / starch	Ø	Ø	Ø	Ø	0	-	0
Grass / cereals	0	0	0	0	0	+	0
Grass / potato	0	0	0	0	0	+	0
Grass / wheat, ground	0	0	0	0	0	+	0
Grass / pomace	0	0	0	0	+	0	0
Grass / starch	Ø	Ø	Ø	Ø	0	-	0
Grass / molasses	0	-	-	0	0	0	0
Grass / water	0	0	-	0	0	0	0
Grass / NFE	0	0	0	-	0	0	0
Molasses / grass	0	-	-	0	0	0	0
Molasses / water	0	0	+	0	0	0	0
Molasses / fiber	0	0	-	0	0	0	0
Starch / cereals	Ø	Ø	Ø	Ø	0	-	0
Starch / potato	Ø	Ø	Ø	Ø	0	-	0
Starch / wheat, ground	Ø	Ø	Ø	Ø	0	-	0
Starch / pomace	Ø	Ø	Ø	Ø	0	-	0
Starch / grass	Ø	Ø	Ø	Ø	0	-	0
Starch / soybean protein	Ø	Ø	Ø	Ø	0	+	0
Starch / NFE	Ø	Ø	Ø	Ø	+	0	0
Soybean protein / potato	Ø	Ø	Ø	Ø	0	+	0
Soybean protein / wheat	Ø	Ø	Ø	Ø	+	-	0
Soybean protein / starch	Ø	Ø	Ø	Ø	0	+	0

Tab.10 (cont'd).

question remains whether the animals used nutritive cues (NFE, protein, energy and fiber), or based their food selection on the components (cereals, potato, straw, soybean solv-extd and rape solv-extd). In section 3.3.3 (p.113) I have made one last attempt to answer this question, exploiting the possibilities of linear programming.

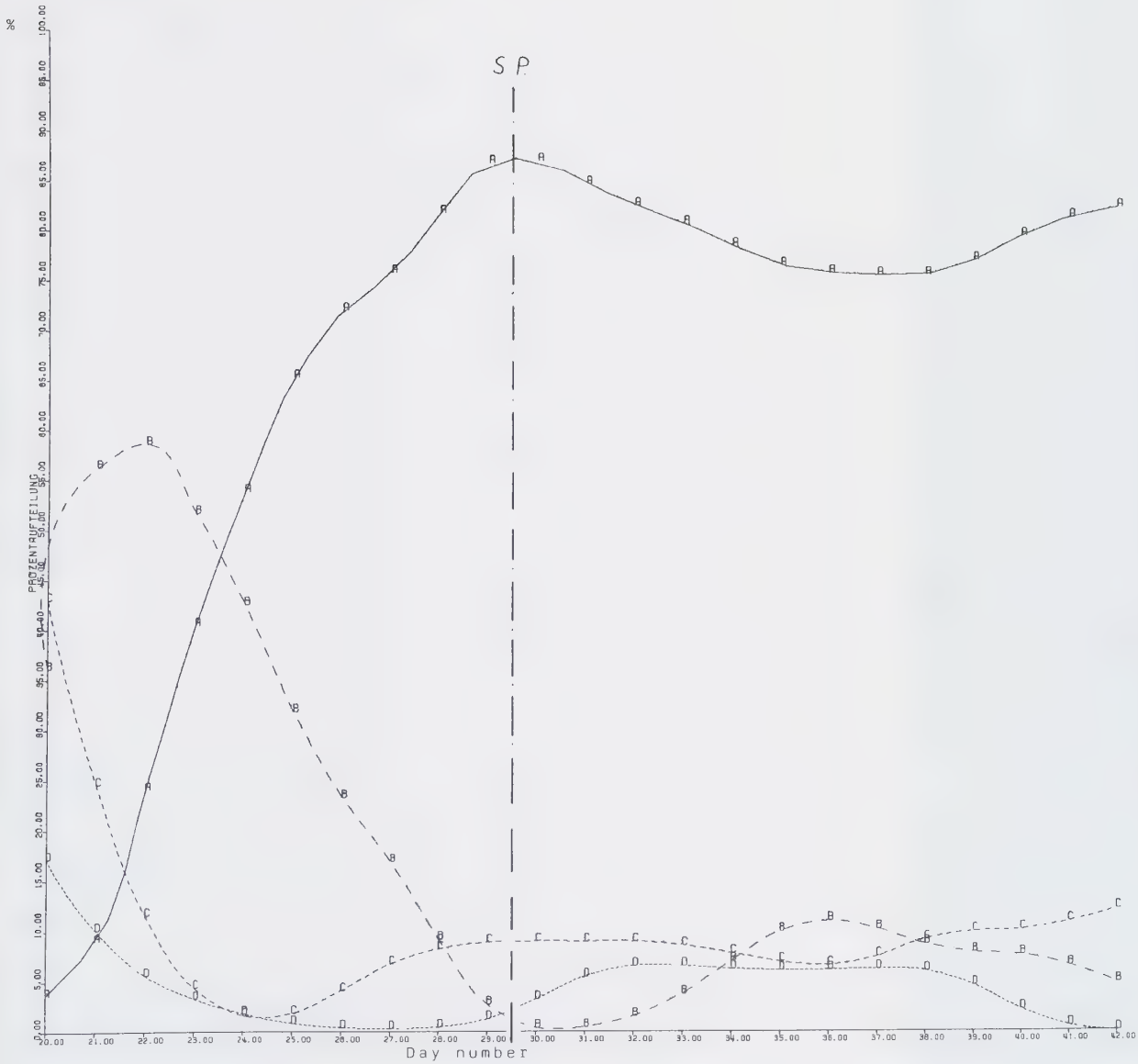

Fig.4a: Percentual intake of pellet types A-D by animal Nr.1, during Food Series II A-D (in % of total pellet weight consumed; smoothed values). S.P. = Stabilization point; E.S.= End of stabilization.

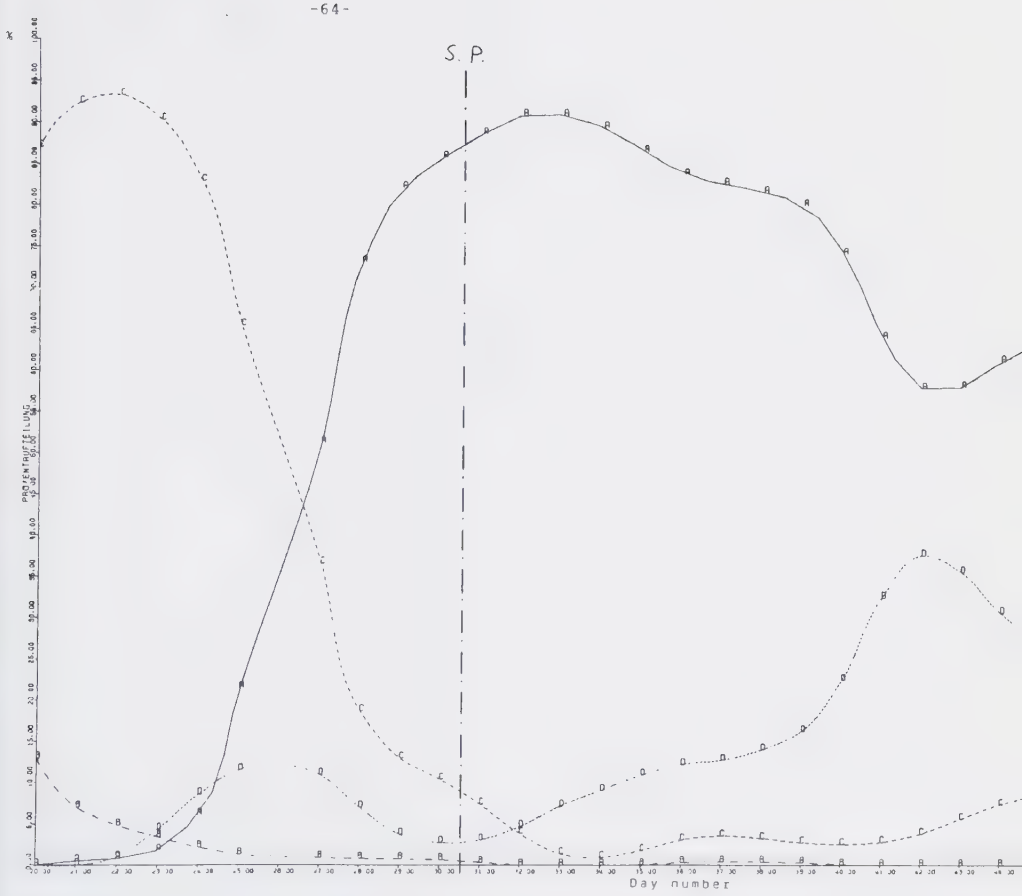

Fig.1b Pellet intake by animal Nr.2 during Series II A-D. (See legend to Fig.4a for this and the following figures).

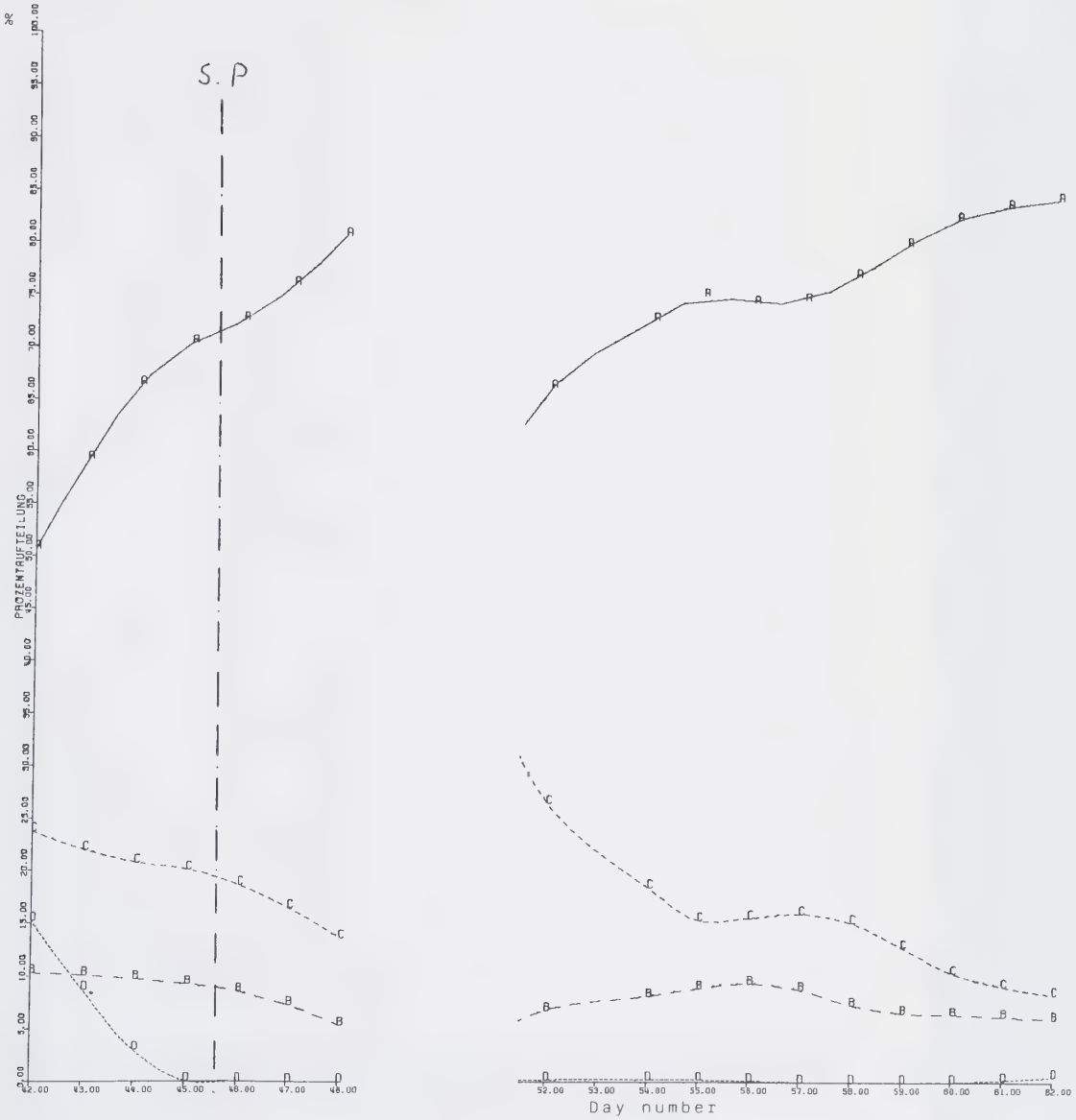

Fig.4c: Pellet intake by animal Nr.3 during Series II A-D.

Fig.4d: Pellet intake by animal Nr.4 during Series II A-D

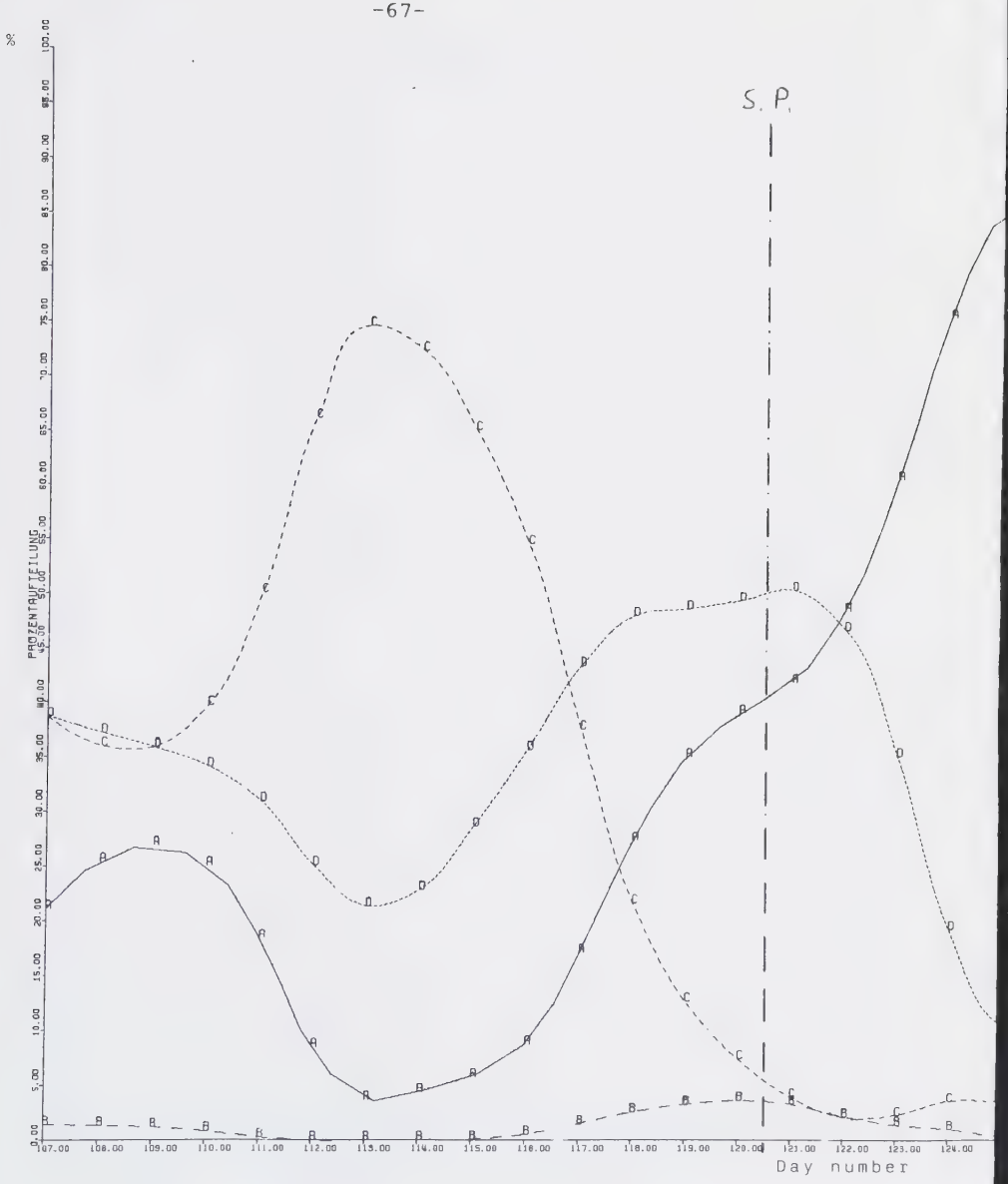

Fig.5a: Pellet intake by animal Nr.1 during Series III A-D

E. S.
128.00
127.00
126.00
129.00
130.00
131.00
132.00
133.00
134.00
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136.00
137.00
138.00
139.00
140.00
141.00
142.00
143.00
144.00

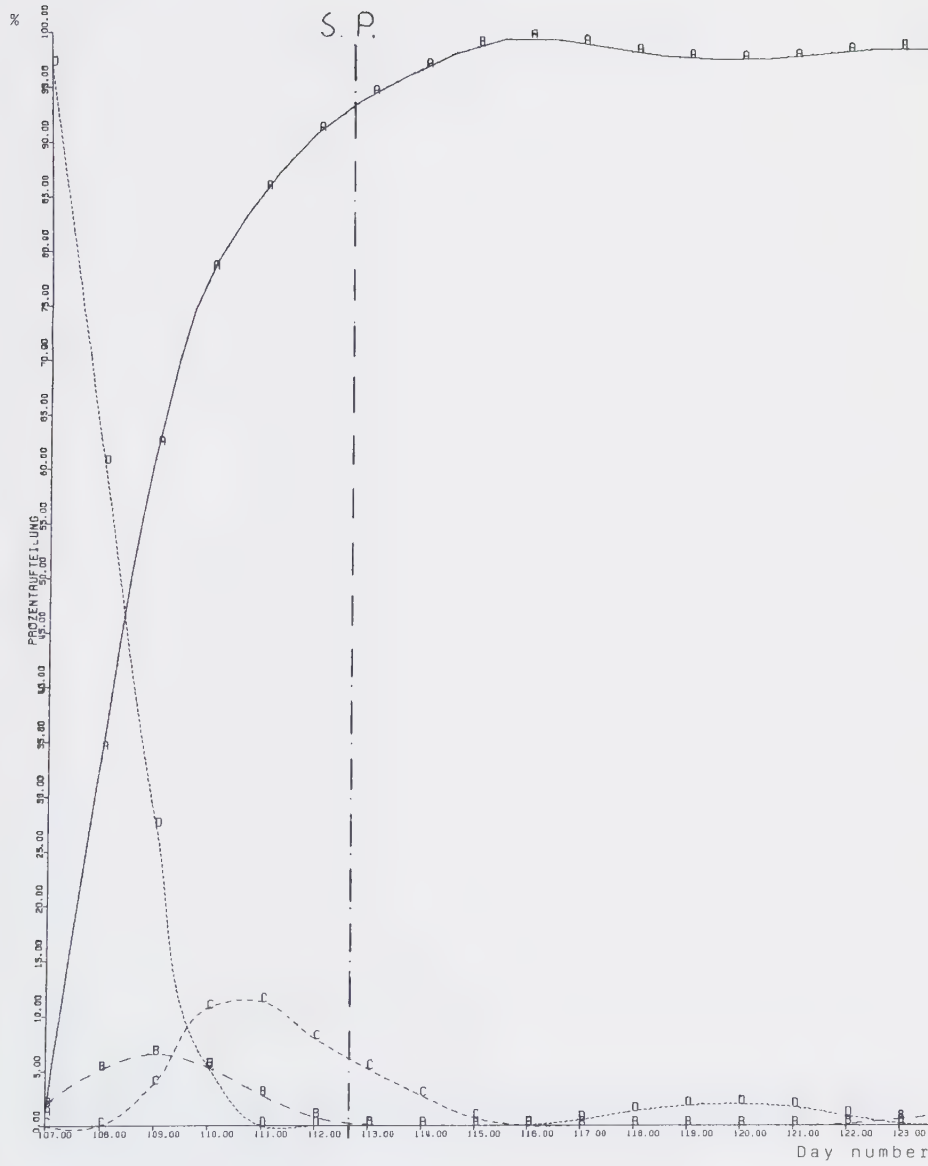


Fig.5b: Pellet intake by animal Nr.2 during Series III A-D.

128.00
127.00
126.00
129.00
130.00
131.00
132.00
133.00
134.00
135.00
136.00
137.00
138.00
139.00
140.00
141.00
142.00
143.00
144.00

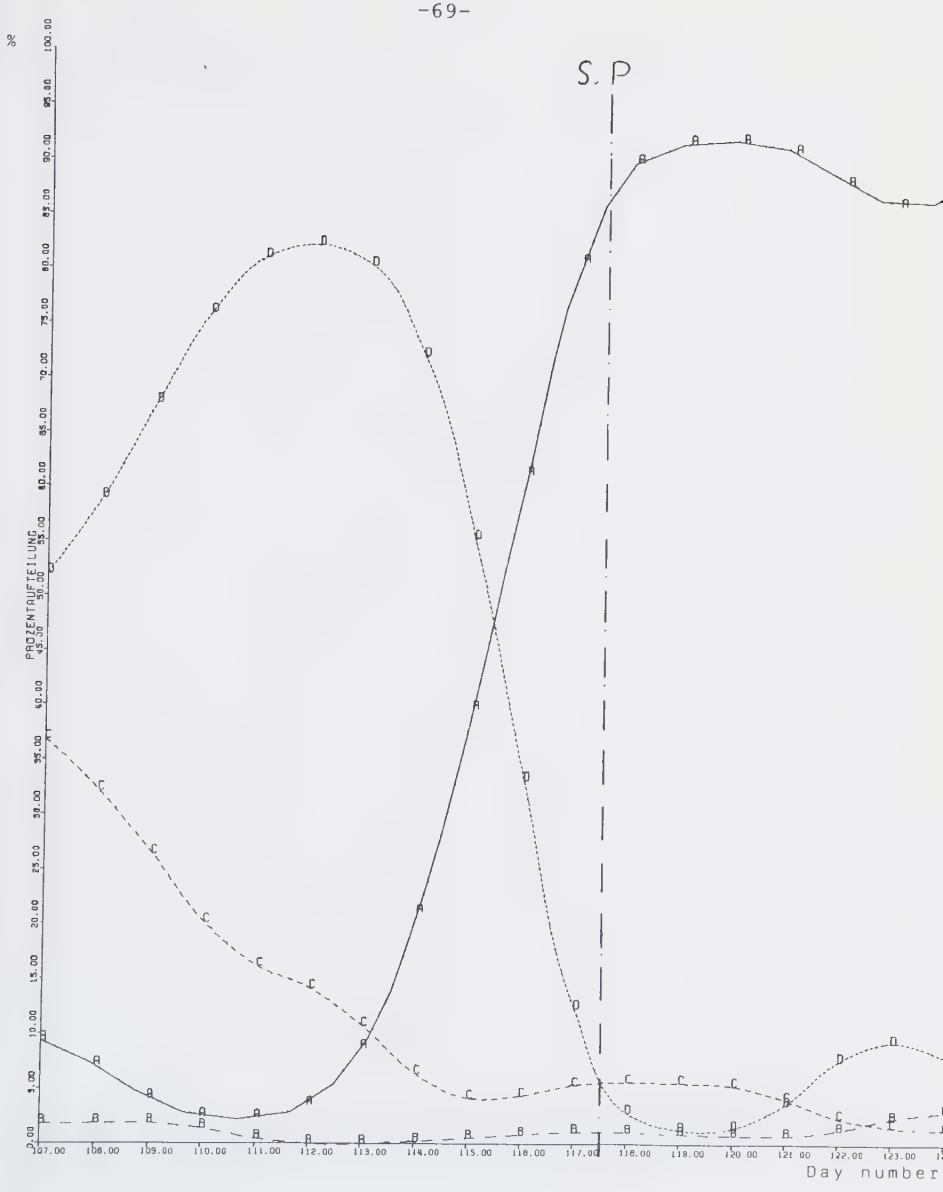
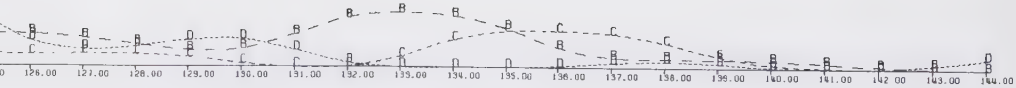


Fig.5c: Pellet intake by animal Nr.3 during Series III A-D.


126.00
127.00
128.00
129.00
130.00
131.00
132.00
133.00
134.00
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137.00
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142.00
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144.00

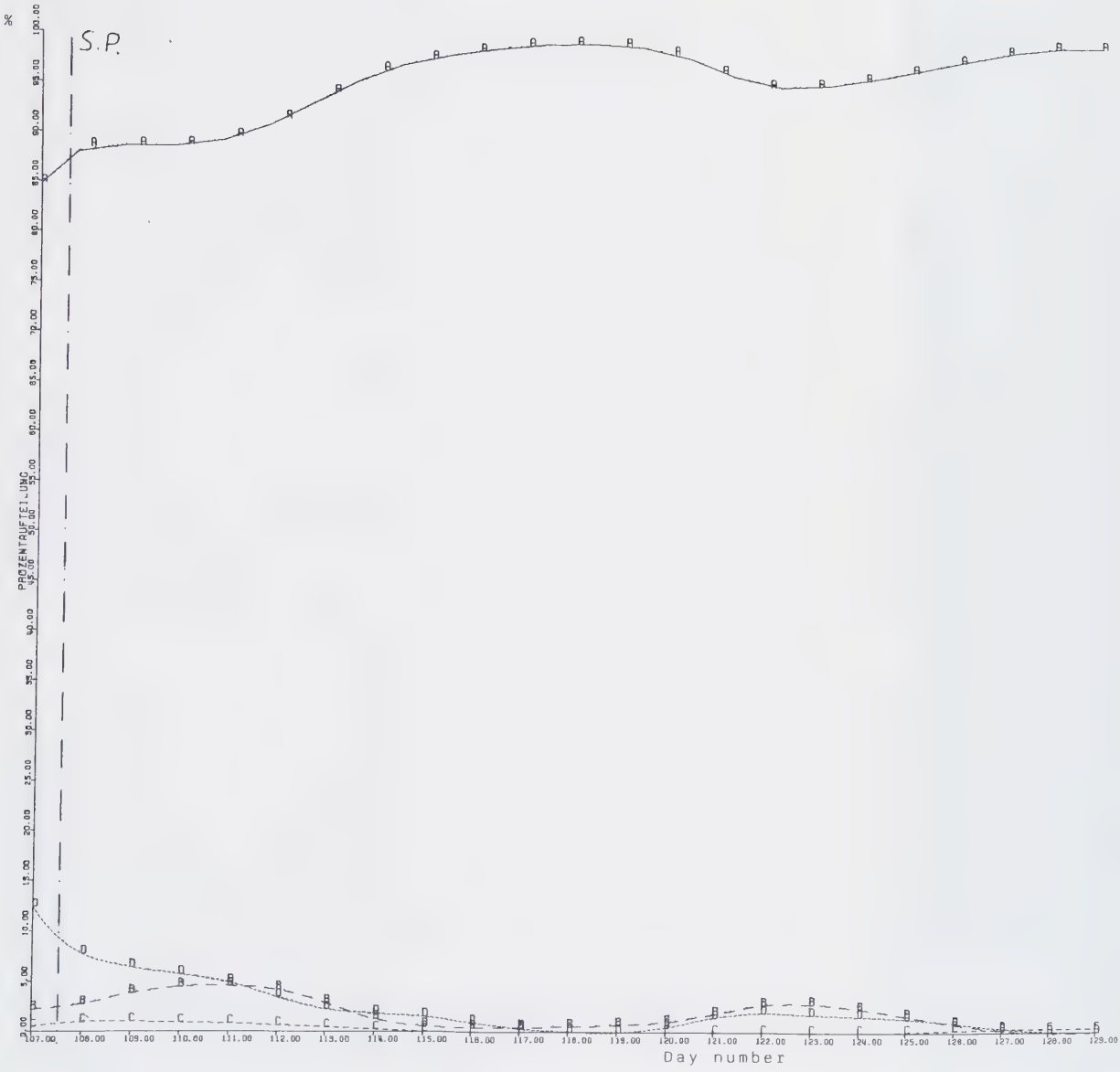


Fig.5d: Pellet intake by animal Nr.4 during Series III A-D.

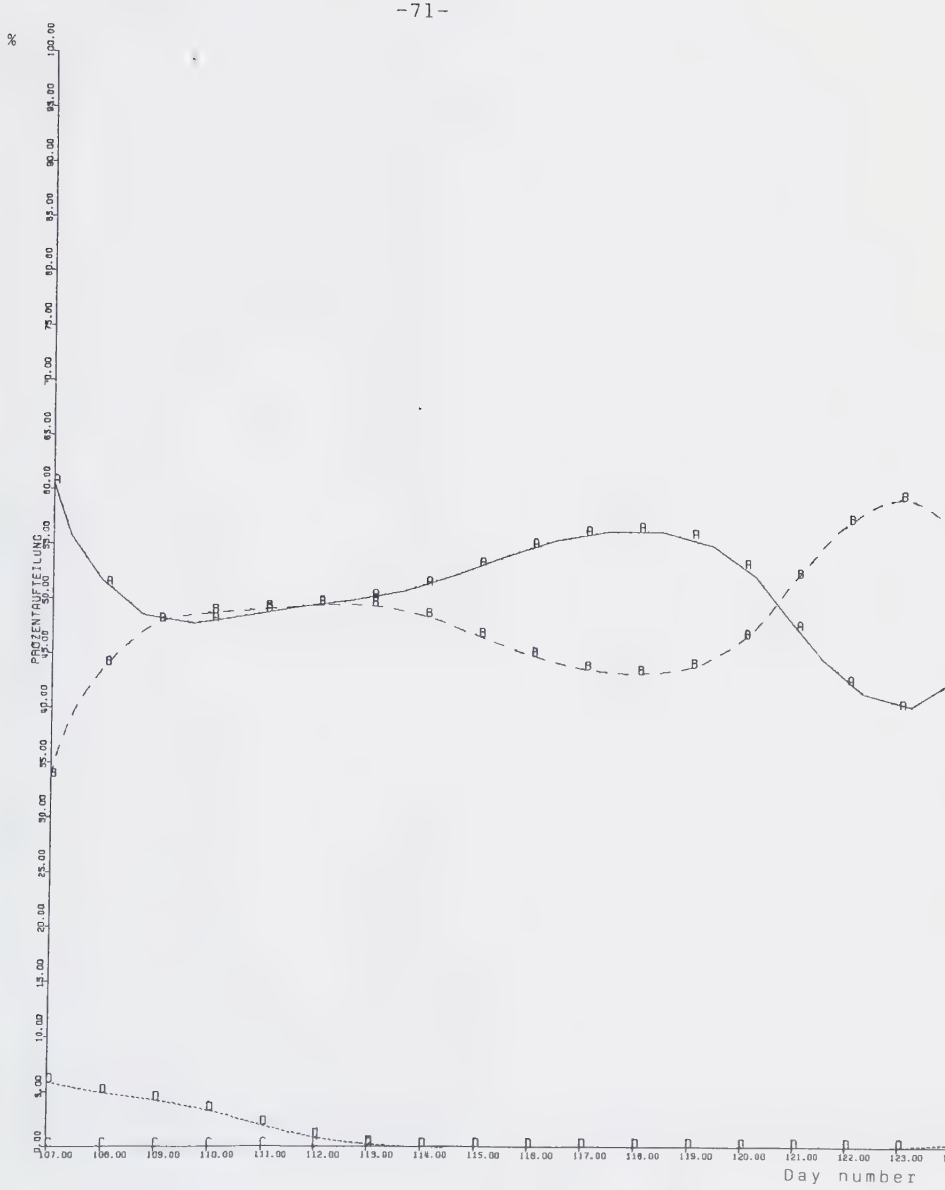
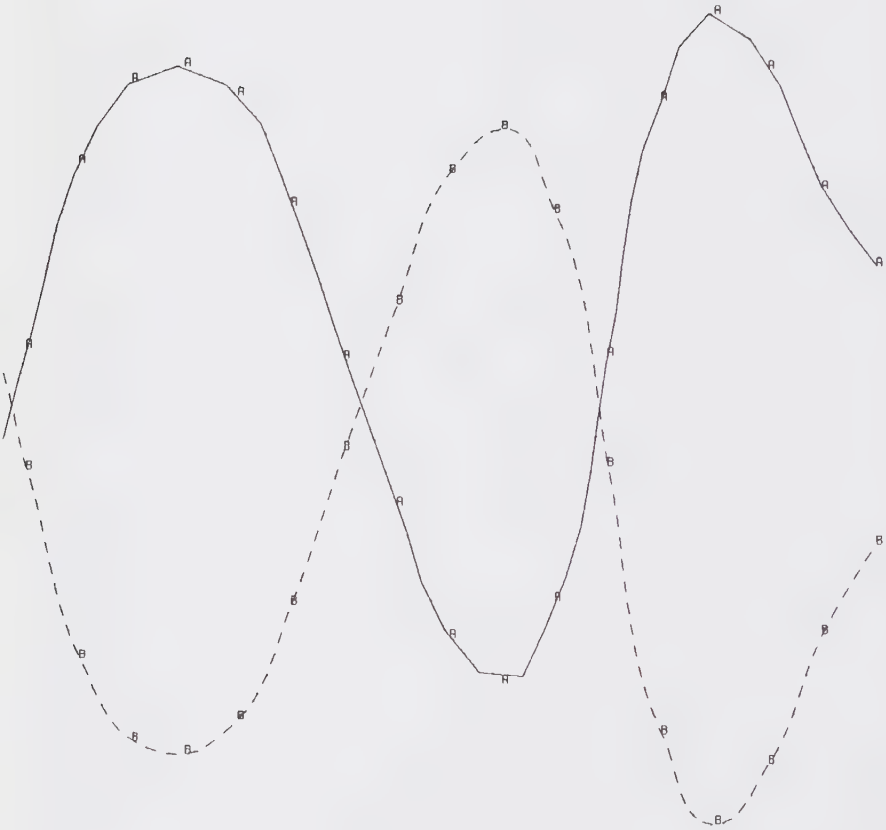


Fig.5e: Pellet intake by animal Nr.5 during Series III A-D.



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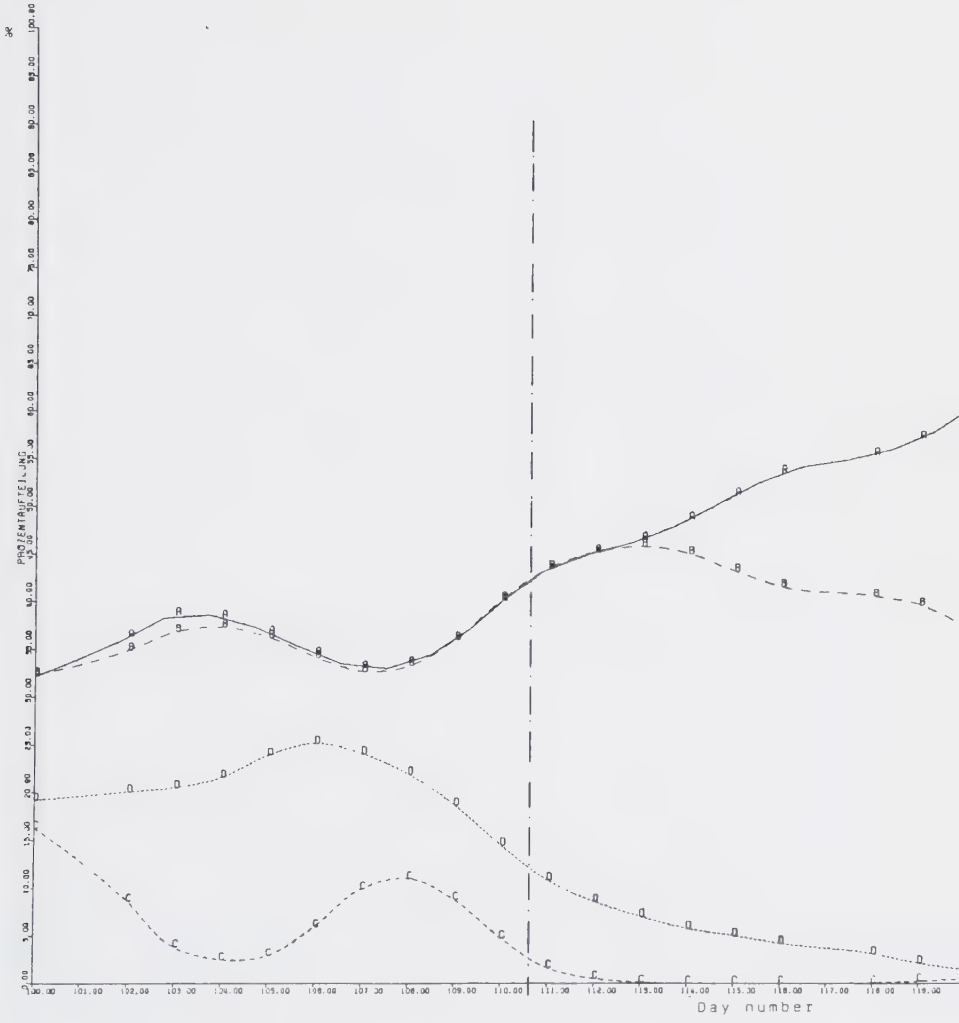
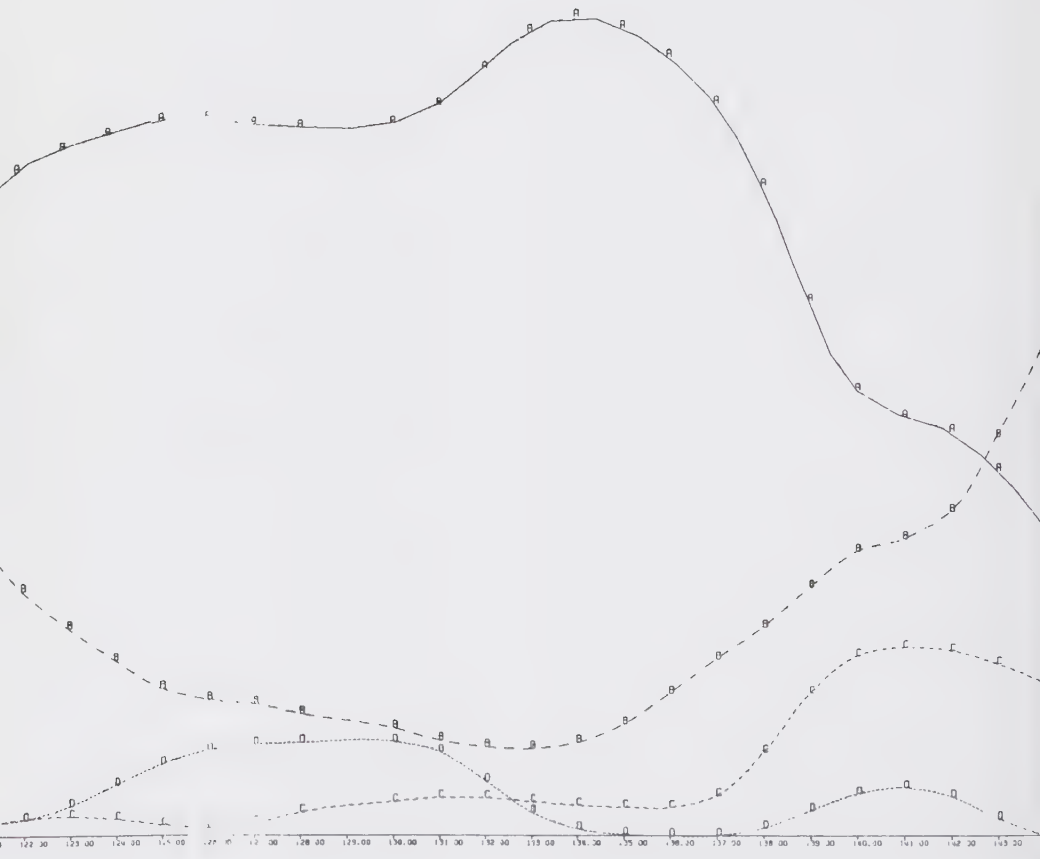


Fig.5f: Pellet intake by animal Nr.6 during Series III A-D.



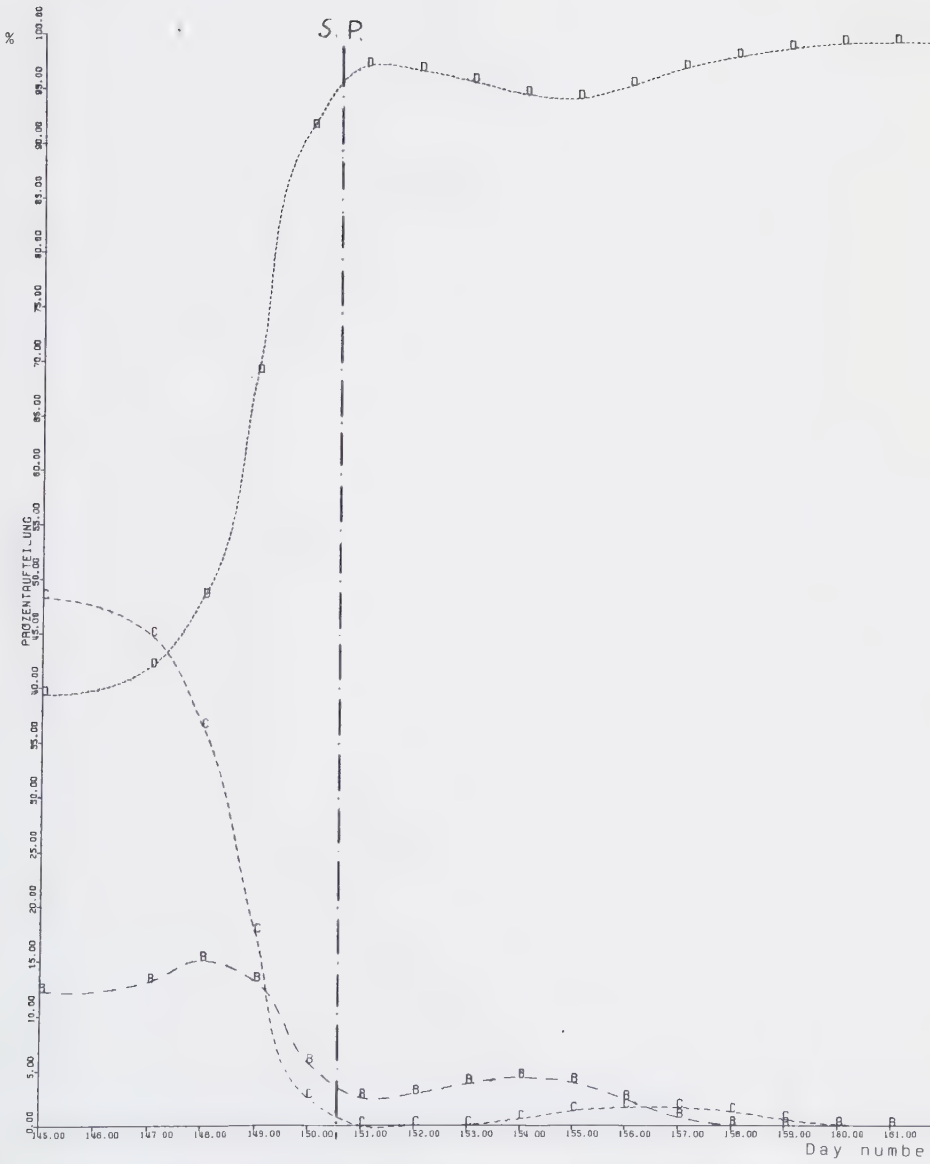


Fig.6a: Pellet intake by animal Nr.1 during Series III B-D.

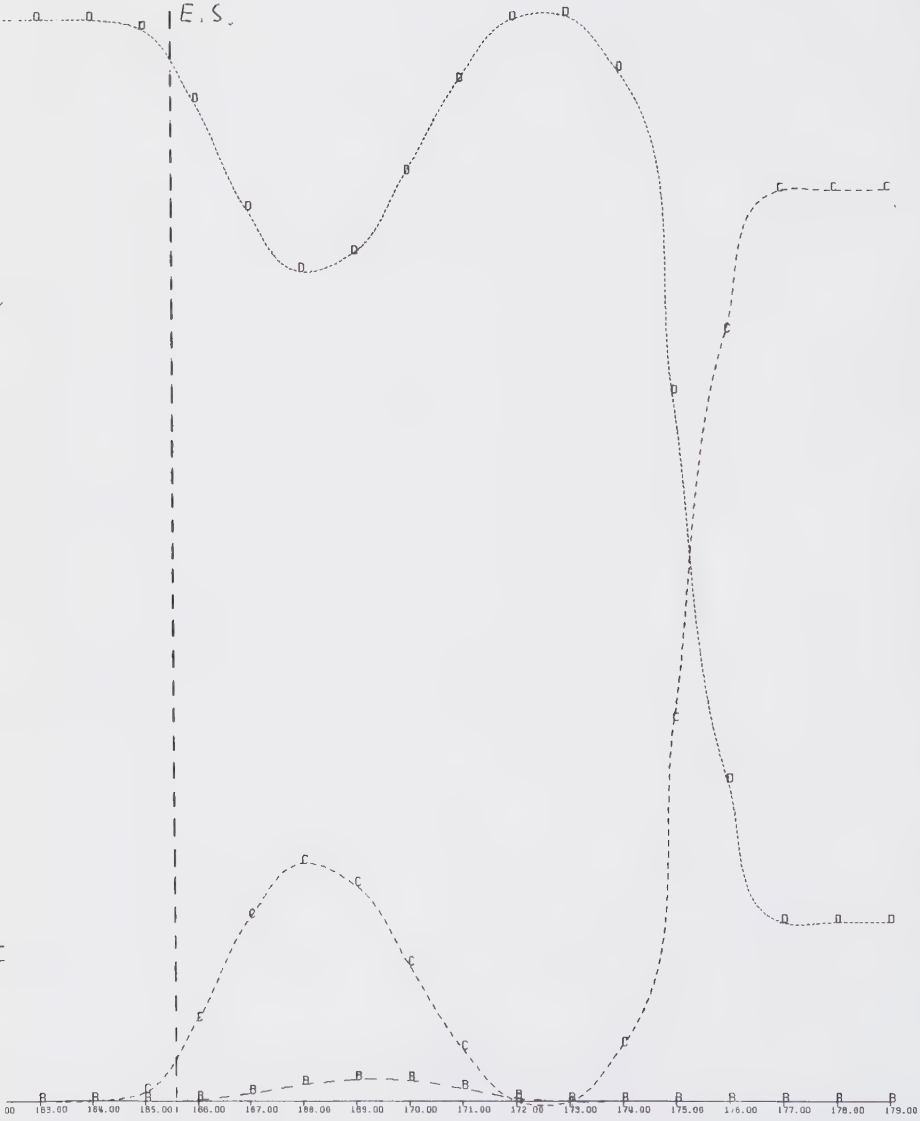

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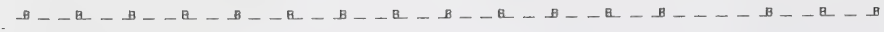
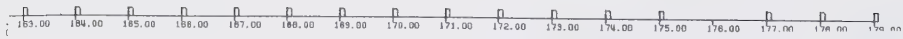
Fig.6b: Pellet intake by animal Nr.2 during Series III B-D.

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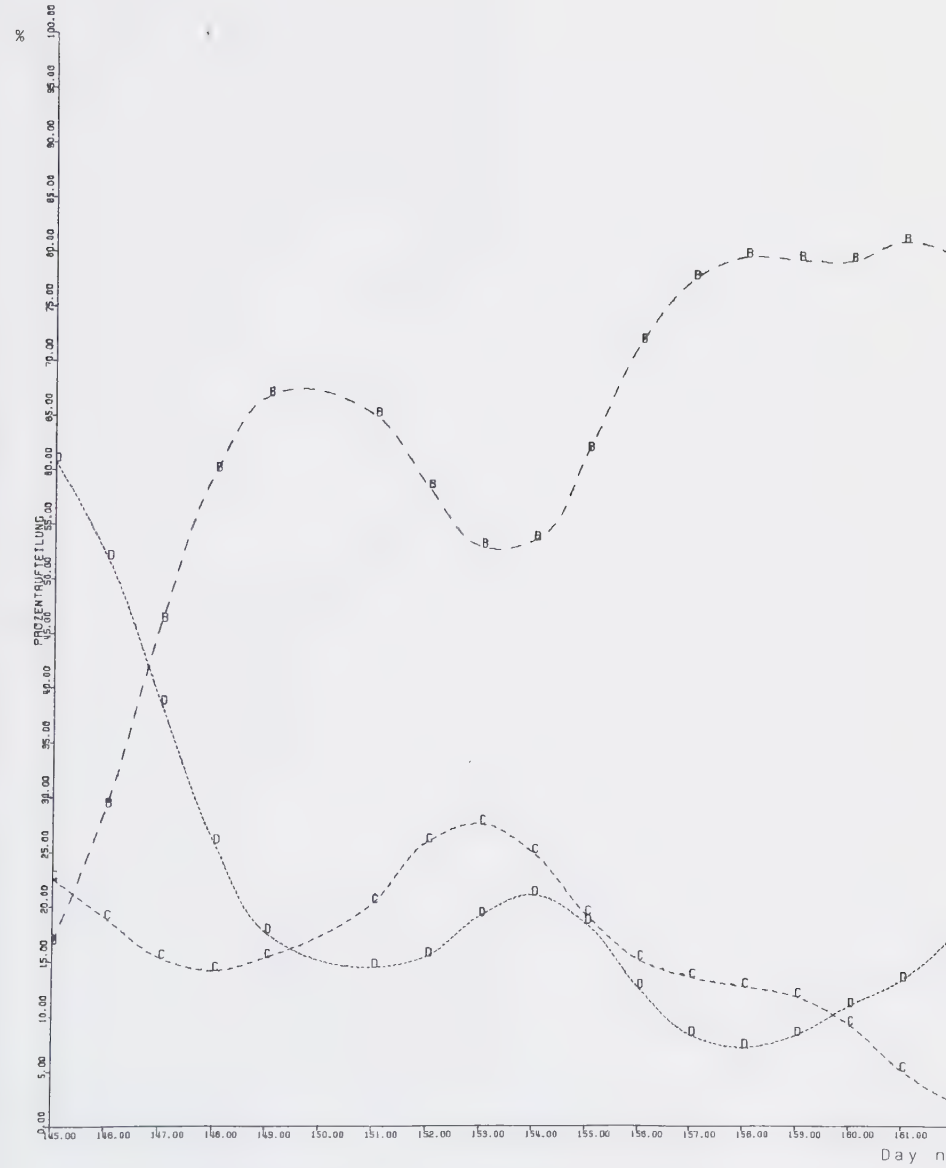
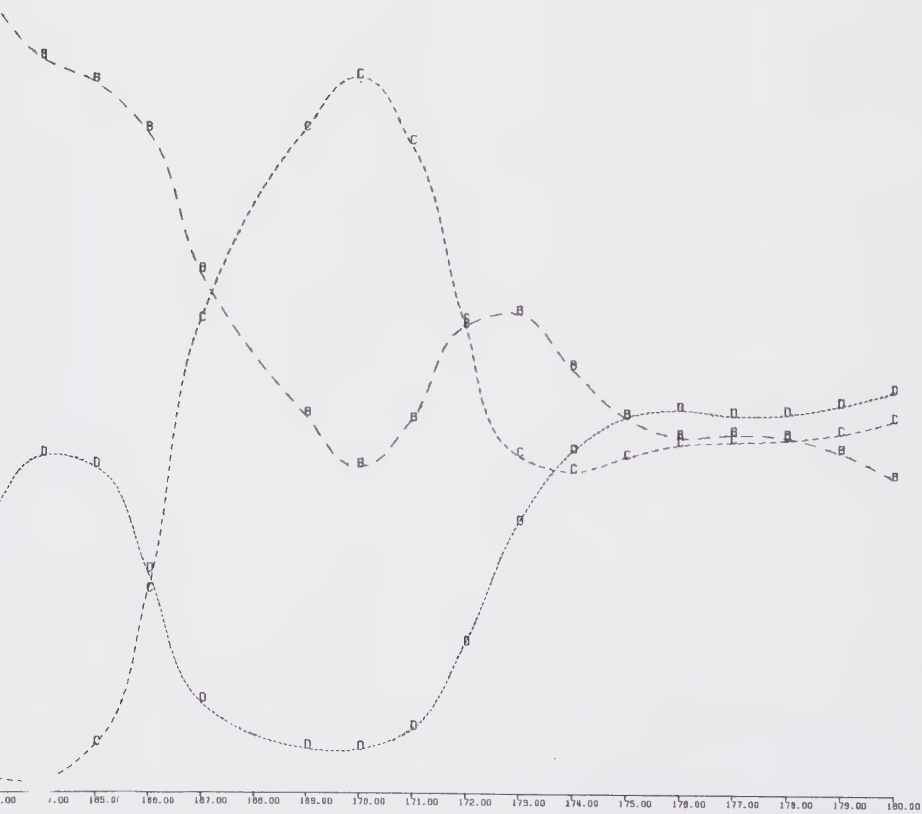


Fig.6c: Pellet intake by animal Nr.3 during Series III B-D.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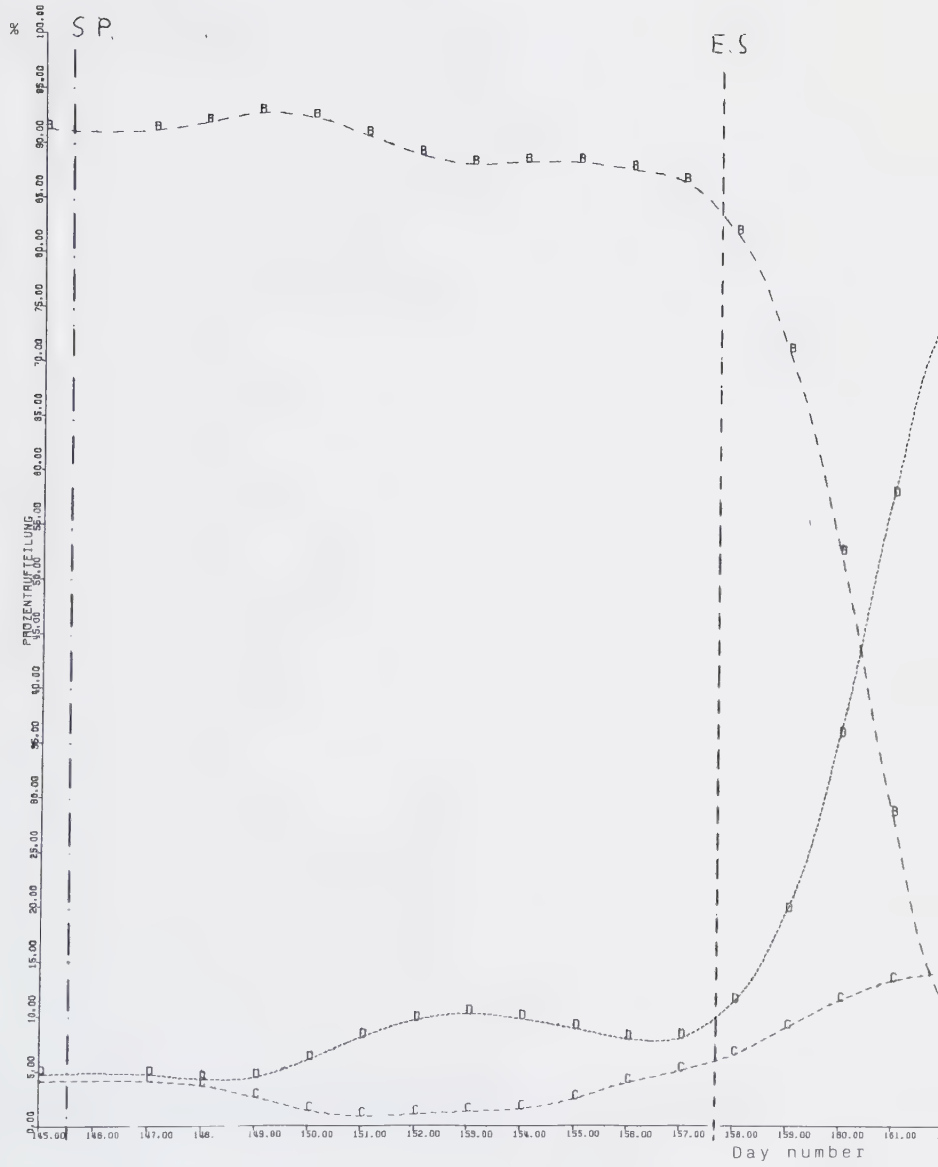

Fig.6d: Pellet intake by animal Nr.4 during Series III B-D.

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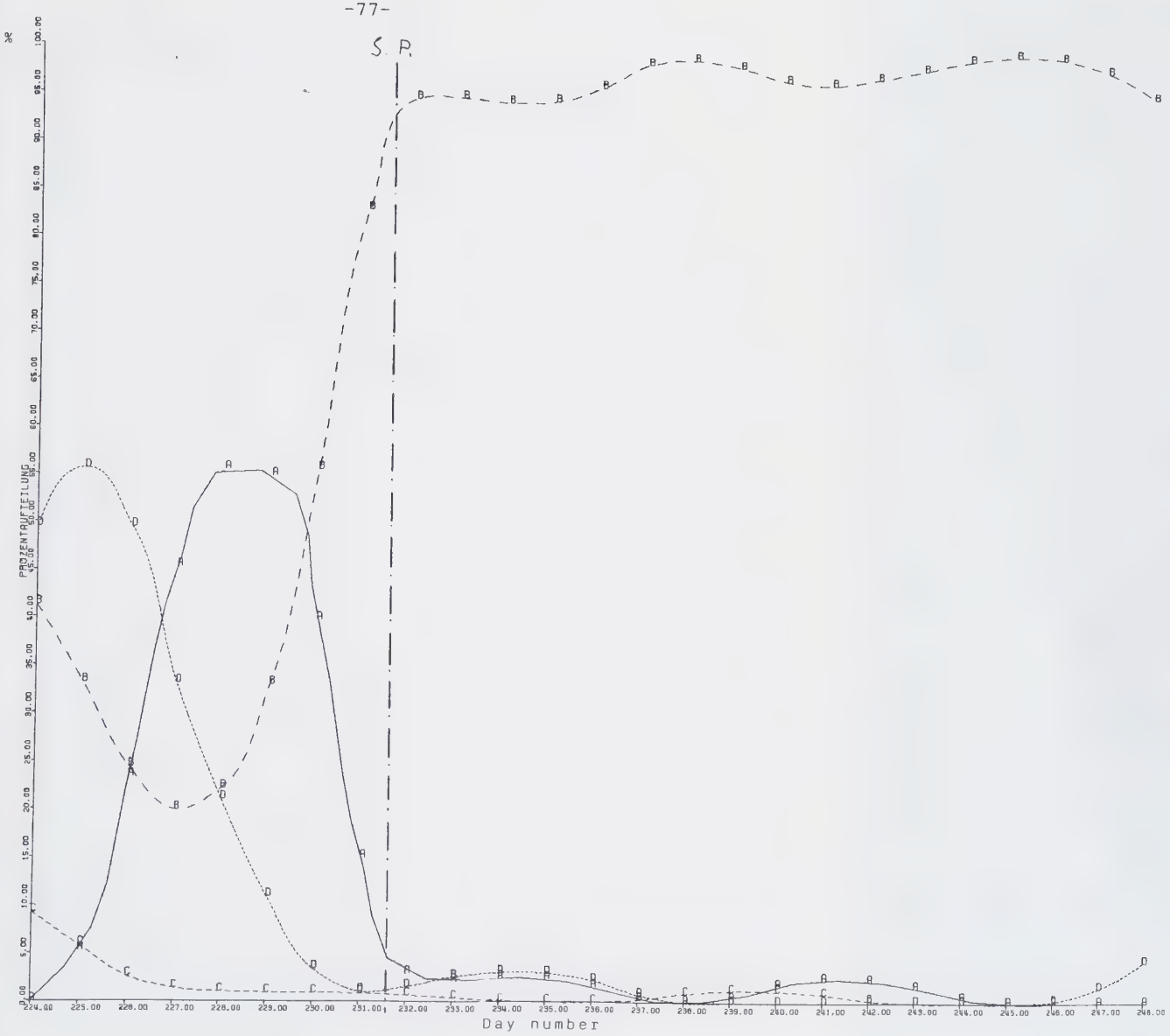


Fig.7a: Pellet intake by animal Nr.1 during Series IV A-D.

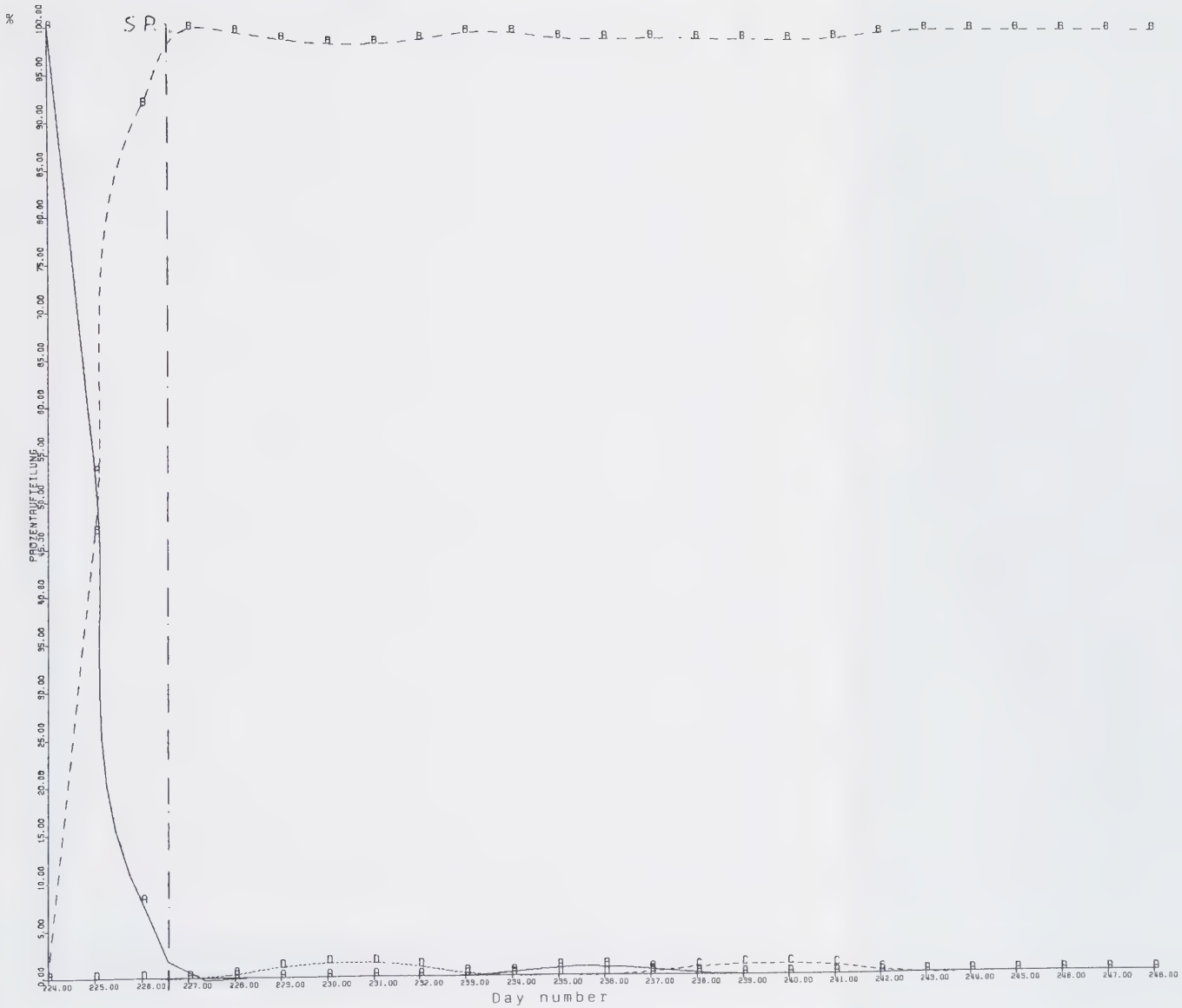


Fig.7b: Pellet intake by animal Nr.2 during Series IV A-D.

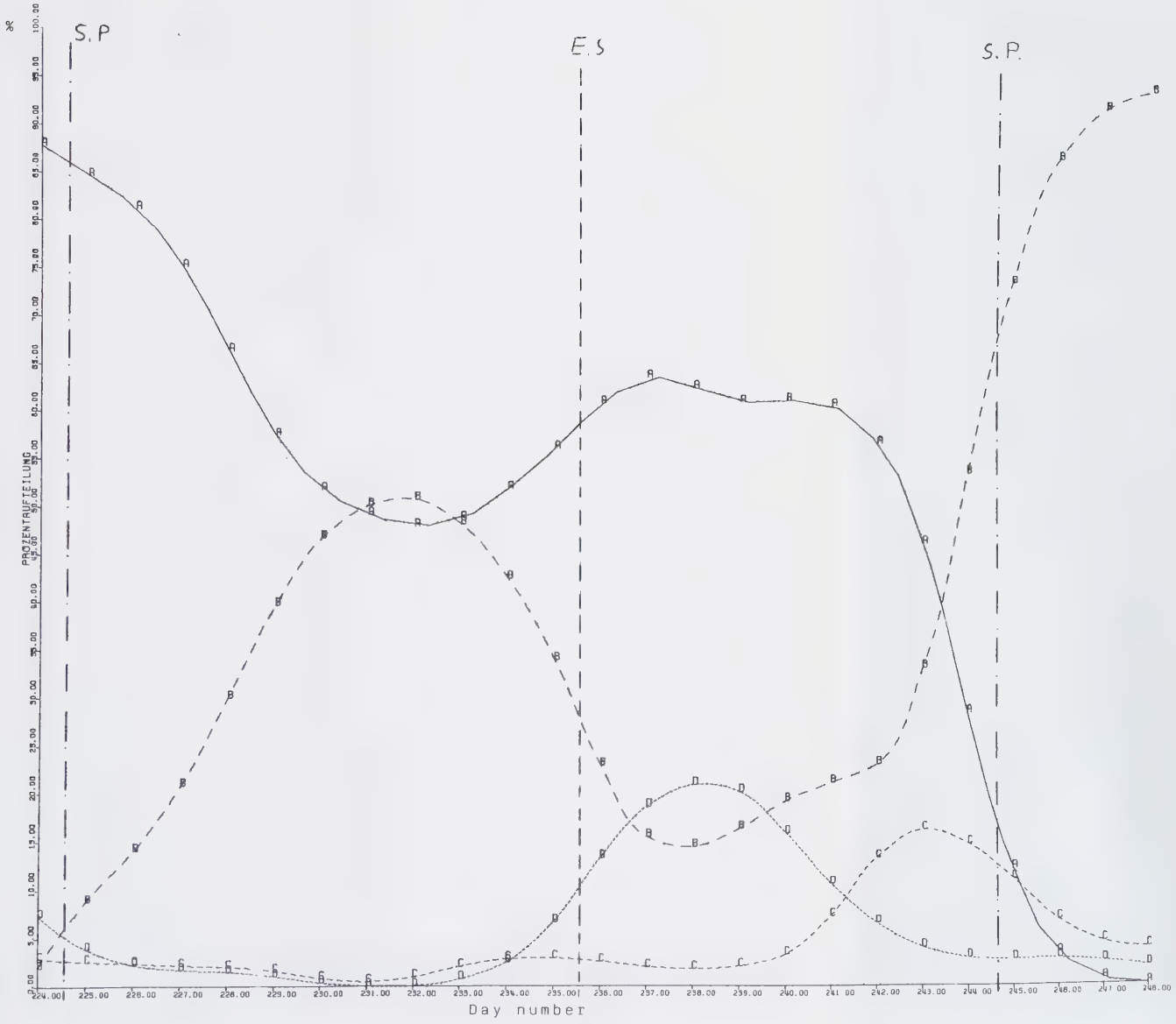


Fig.7c: Pellet intake by animal Nr.3 during Series IV A-D.

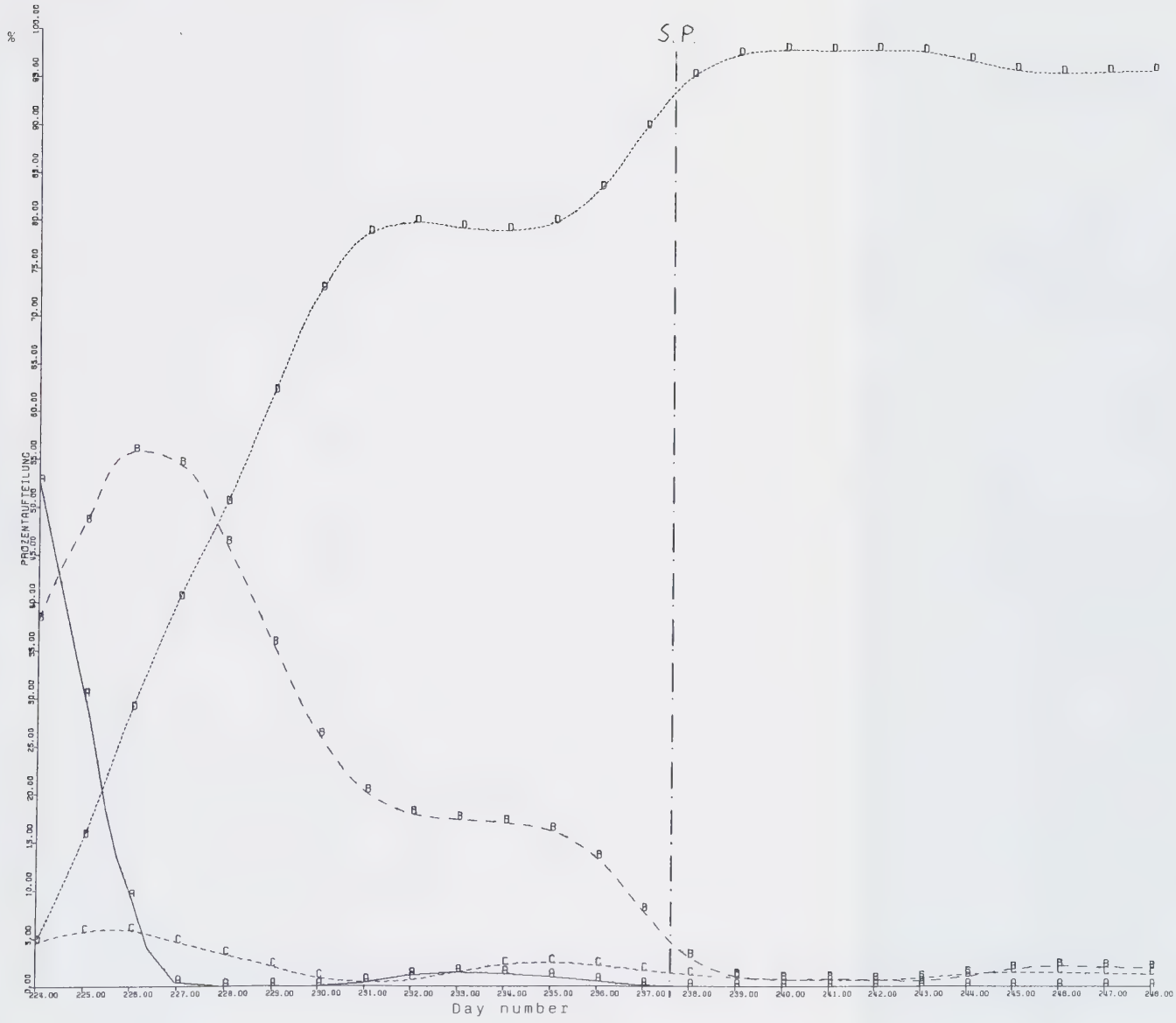


Fig.7d: Pellet intake by animal Nr.4 during Series IV A-D.

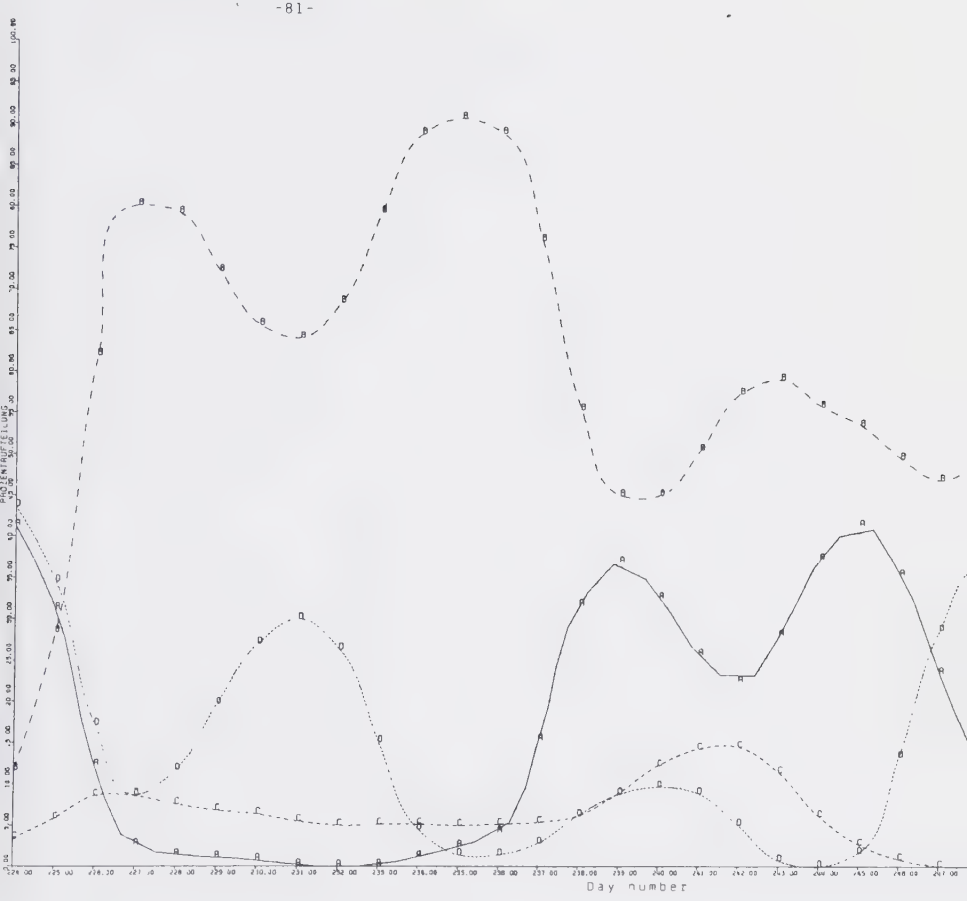
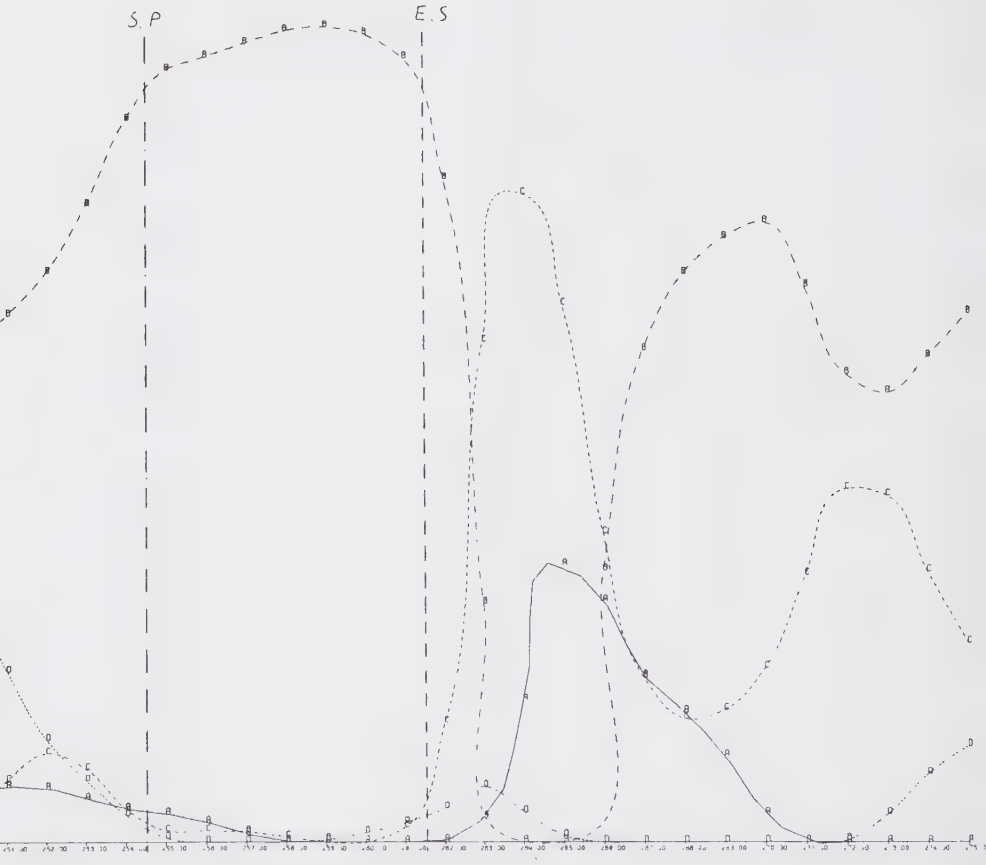


Fig. 5 Pellet intake by animal Nr.9 during Series IV A-D.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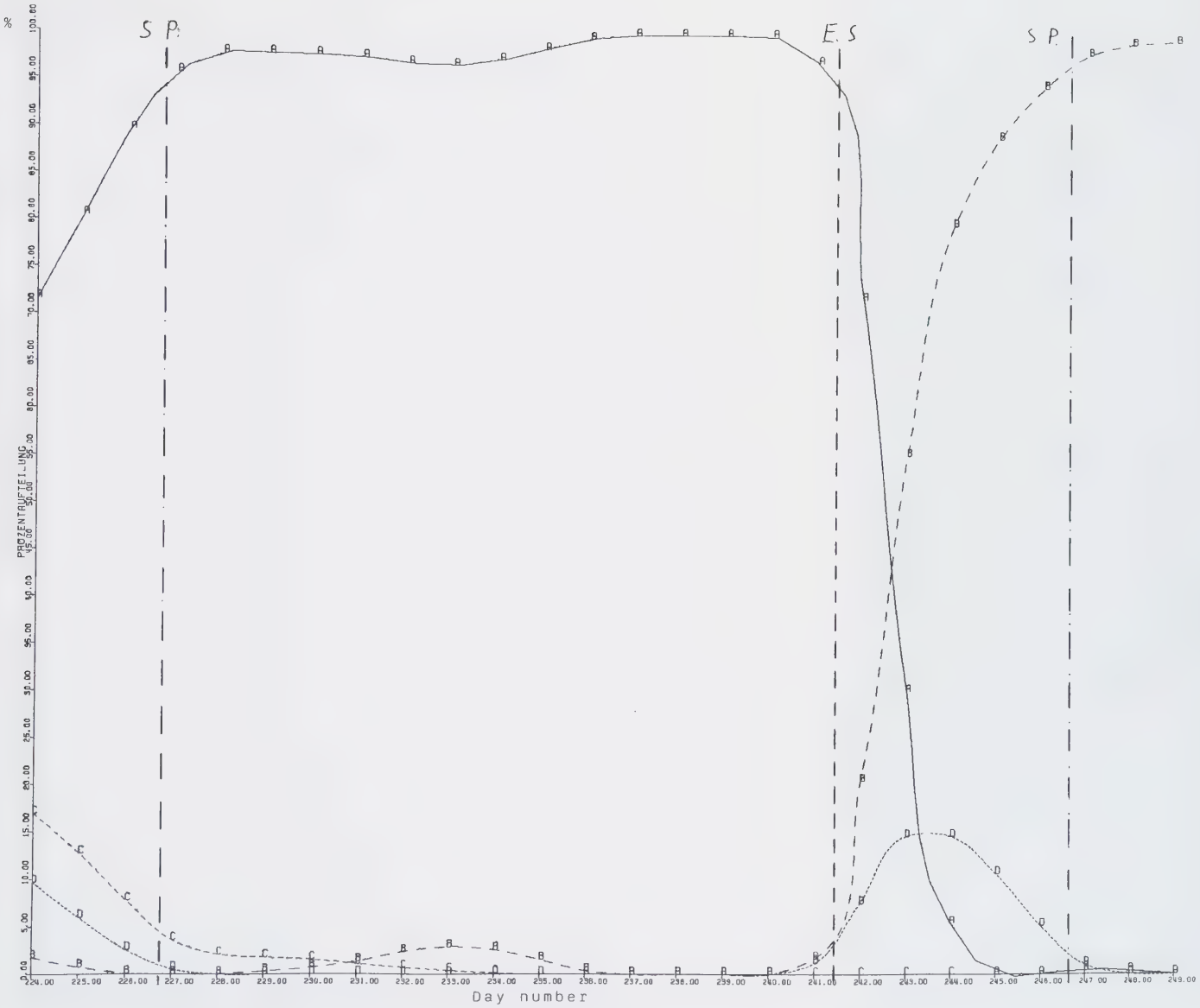


Fig.7f: Pellet intake by animal Nr.10 during Series IVA-D.

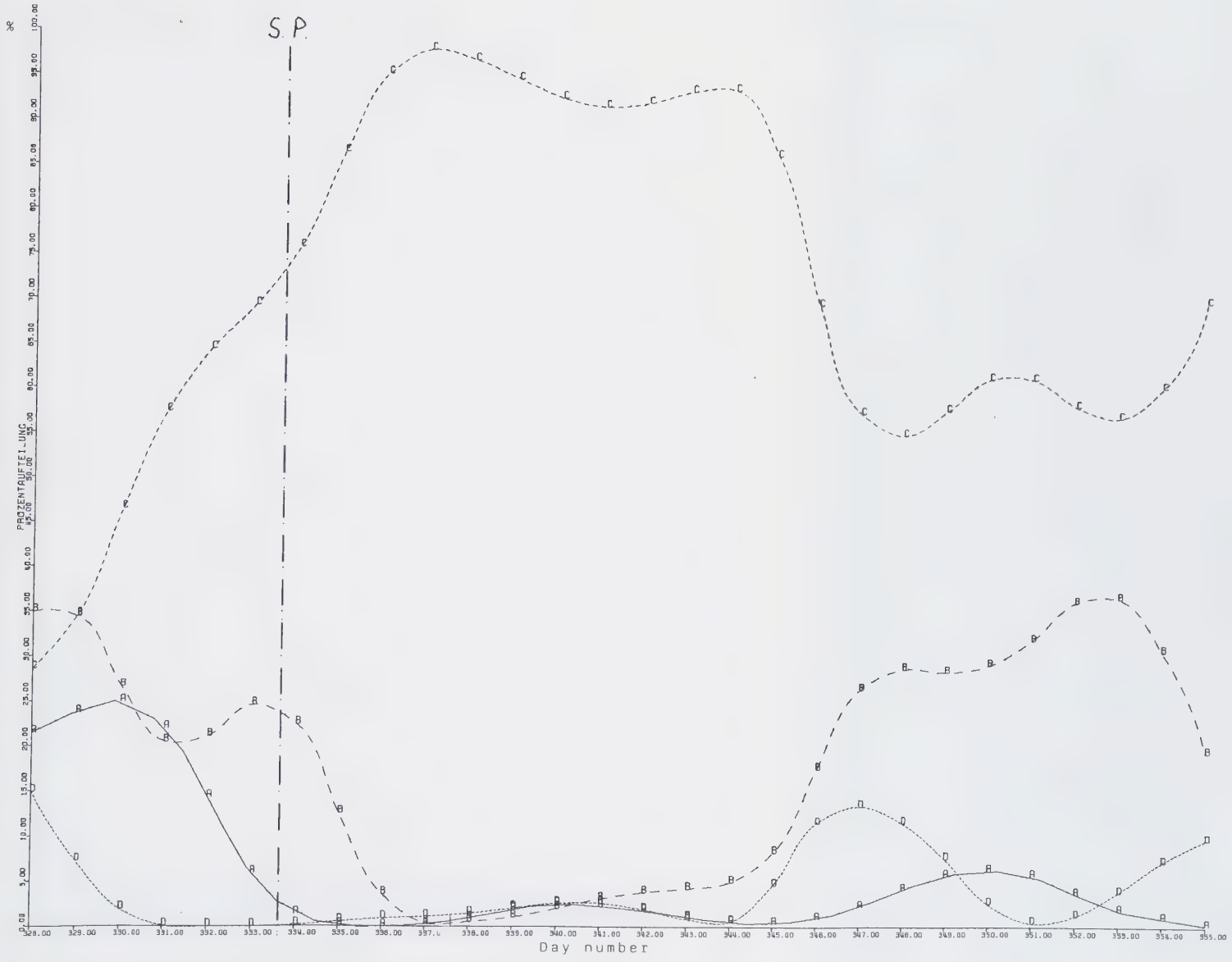


Fig.8a: Pellet intake by animal Nr.1 during Series V A-D.

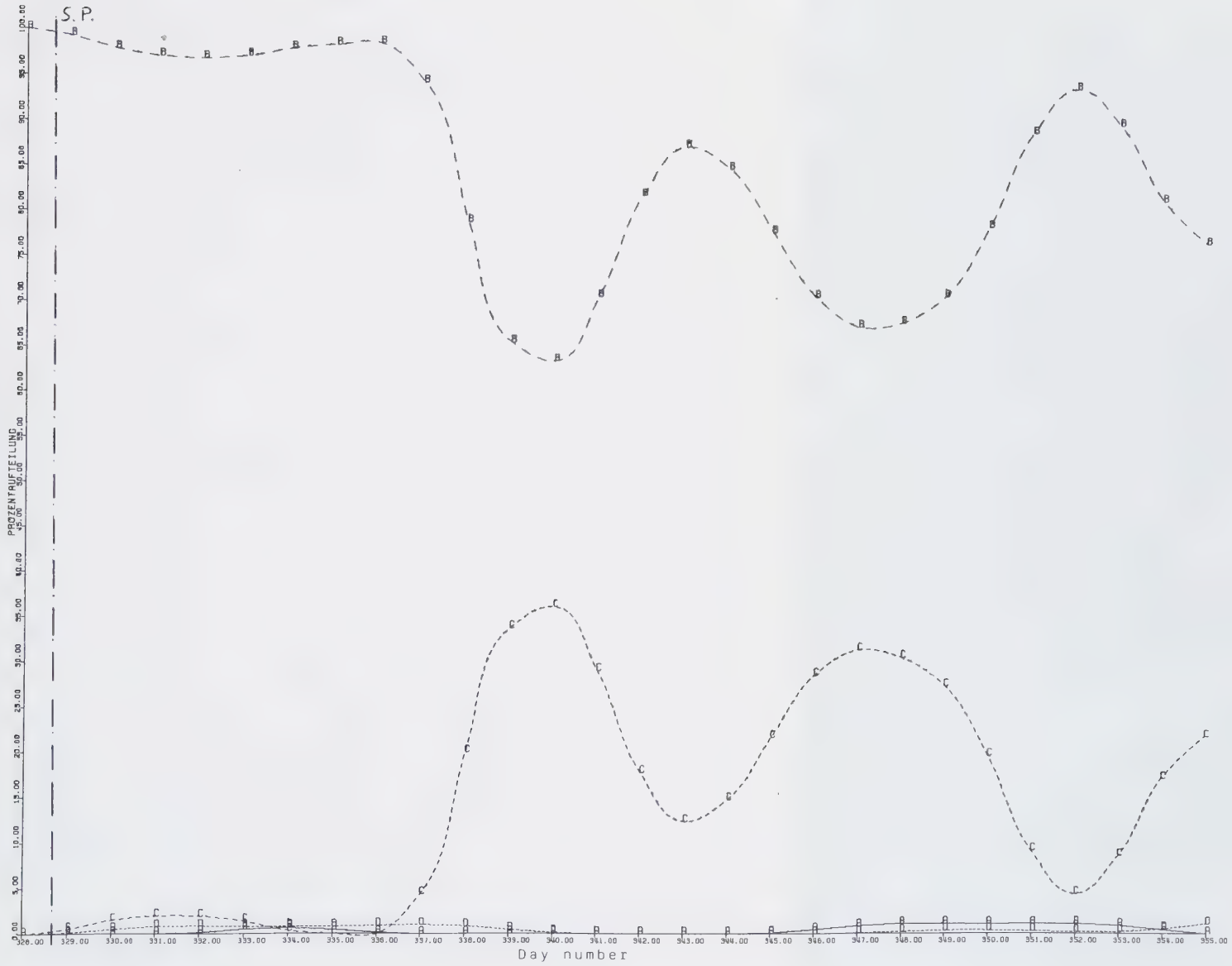


Fig.8b: Pellet intake by animal Nr.2 during Series V A-D.

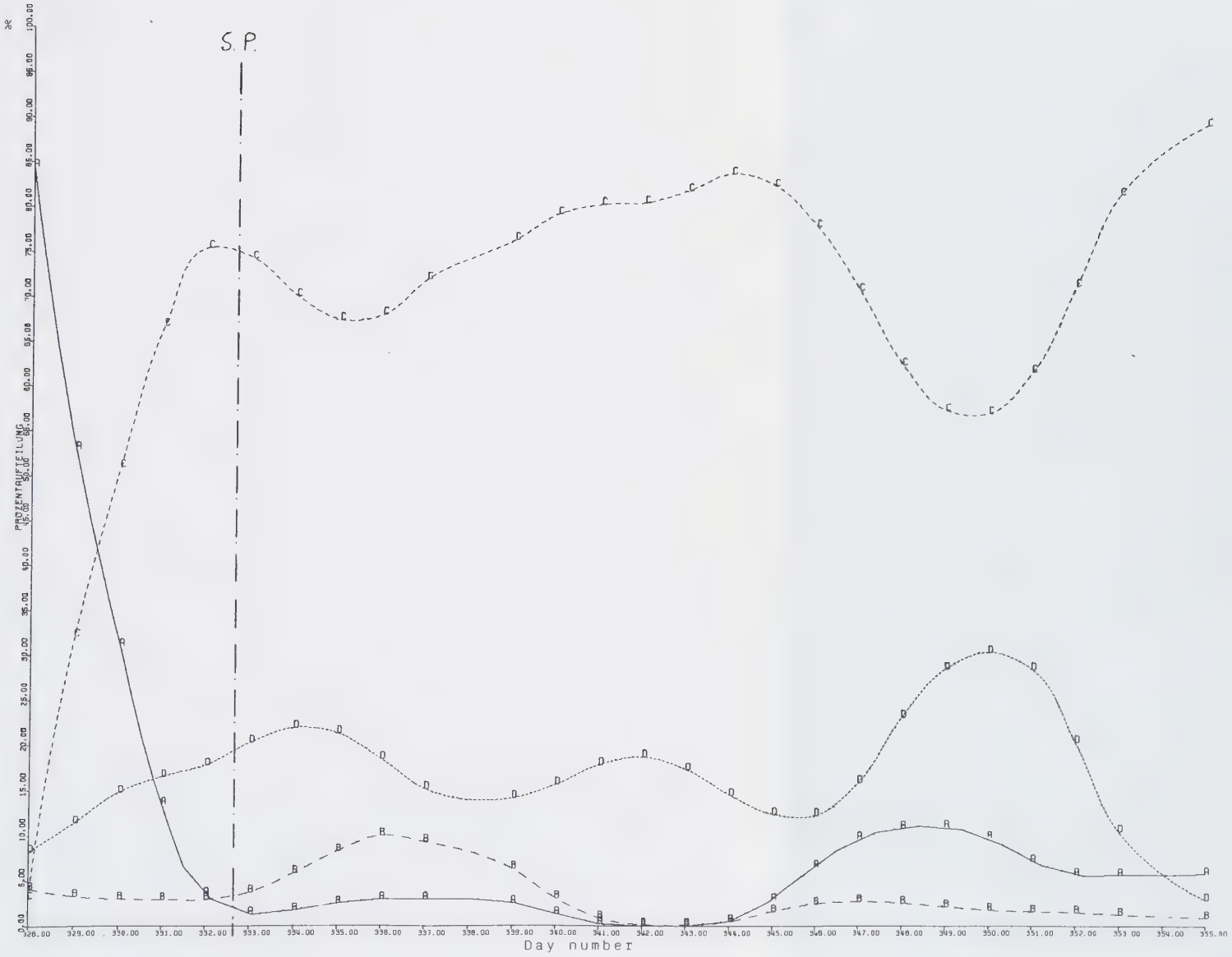


Fig.8c: Pellet intake by animal Nr.3 during Series V A-D.

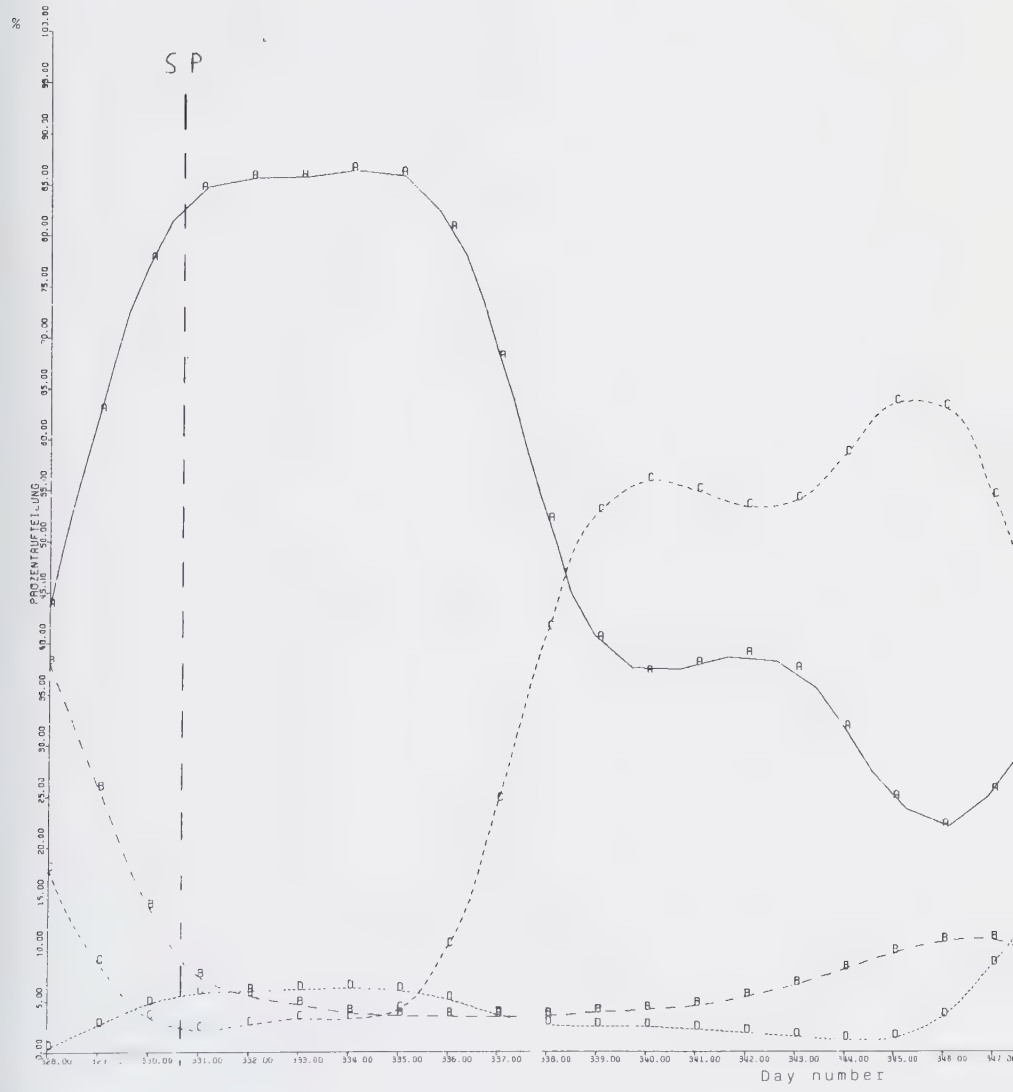
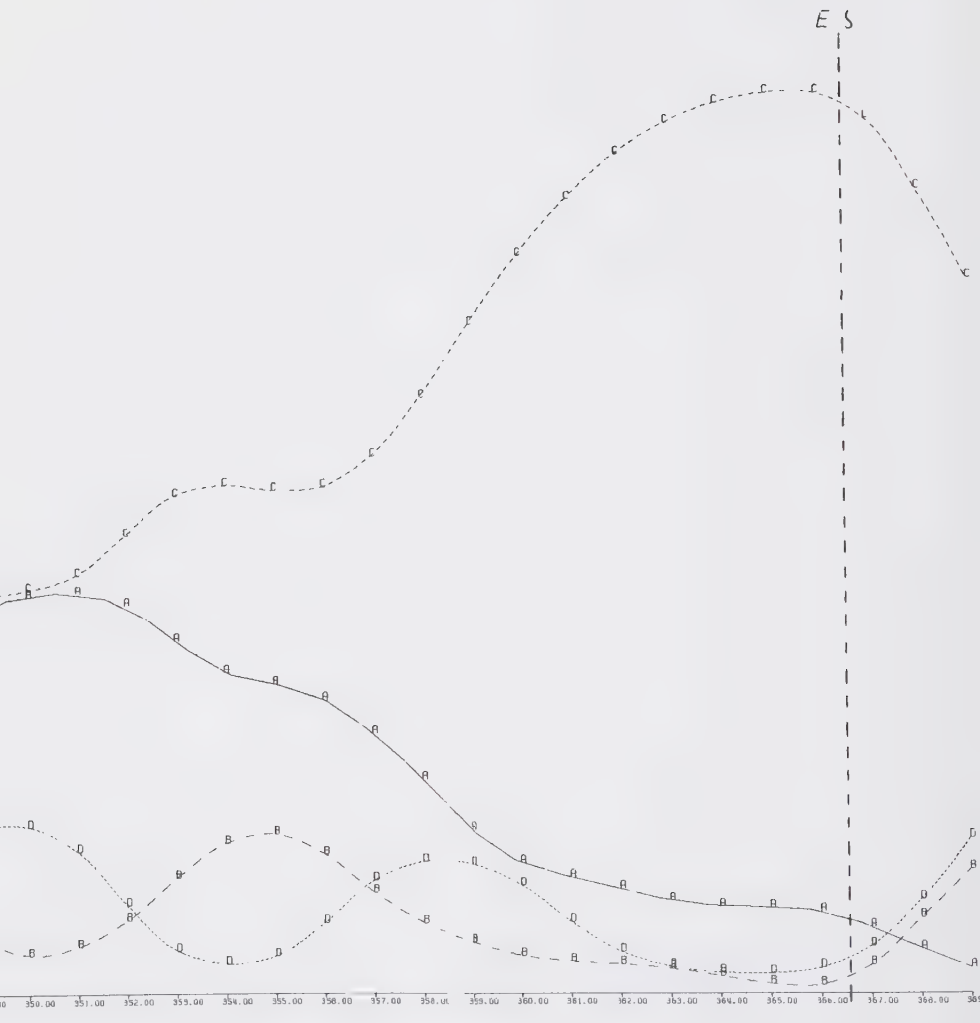


Fig.31 Pellet intake by animal Nr.4 during Series V A-D.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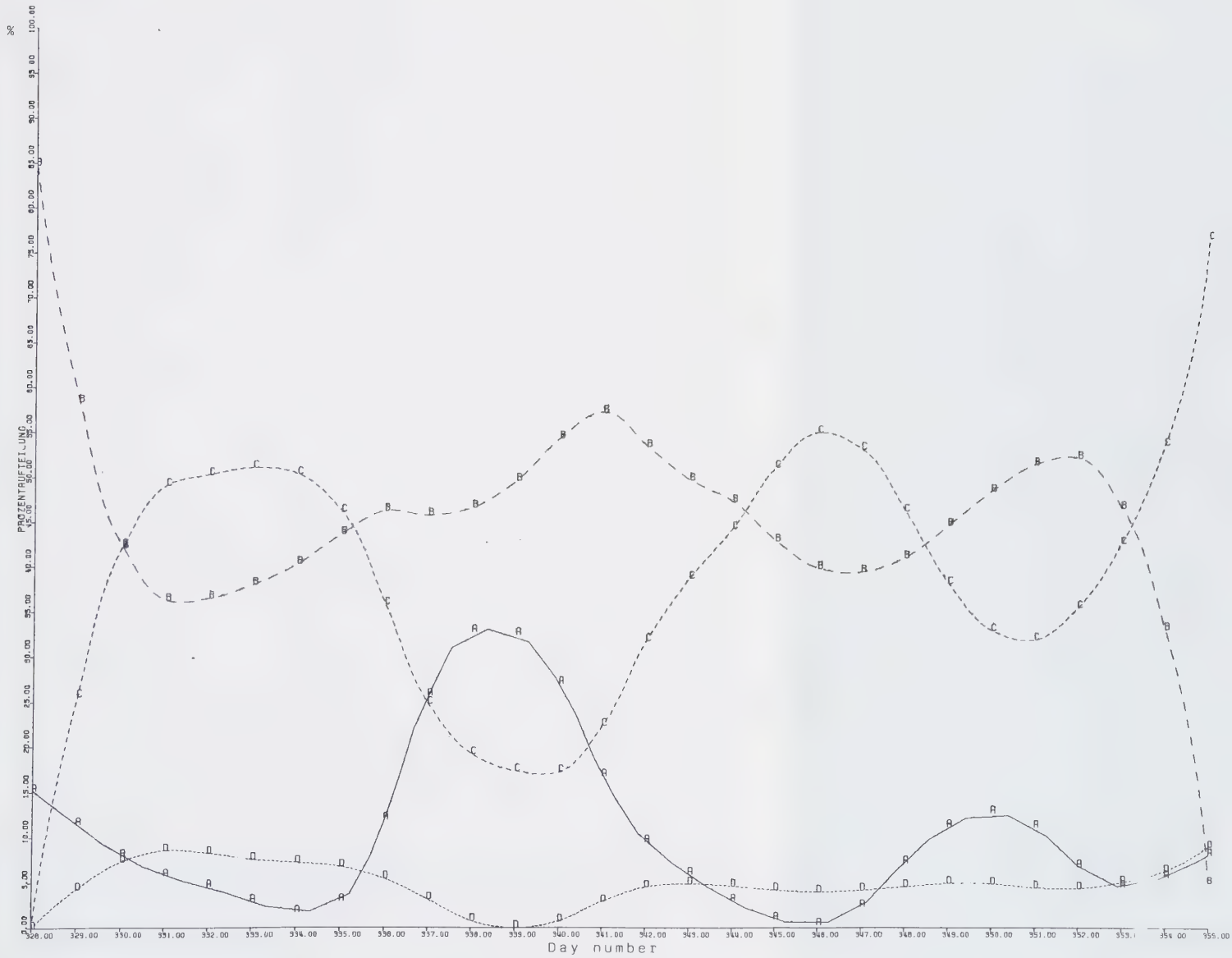
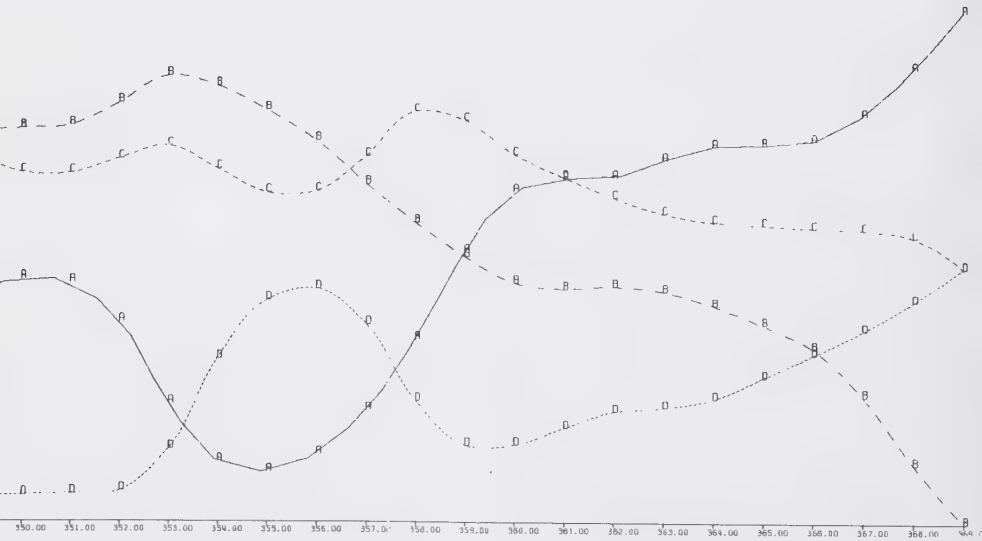


Fig.8e: Pellet intake by animal Nr.9 during Series V A-D.

g.4f: Pellet intake by animal Nr.10 during Series V A-D.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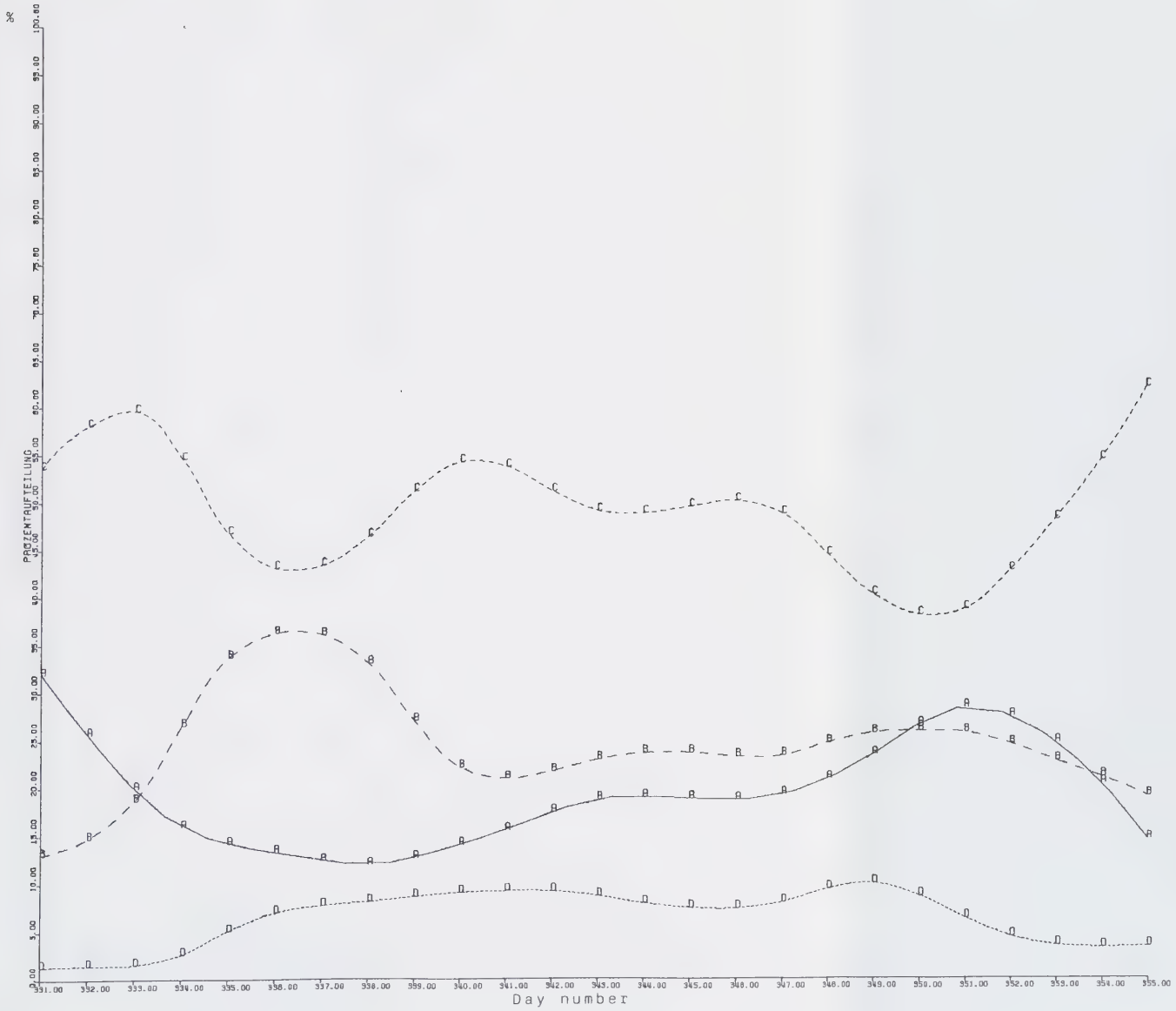


Fig.8g: Pellet intake by animal Nr.5 during Series V A-D.

Fig.8h: Pellet intake by animal Nr.6 during Series V A-D.

Fig.9a: Pellet intake by animal Nr.1 during Series VI A-D.

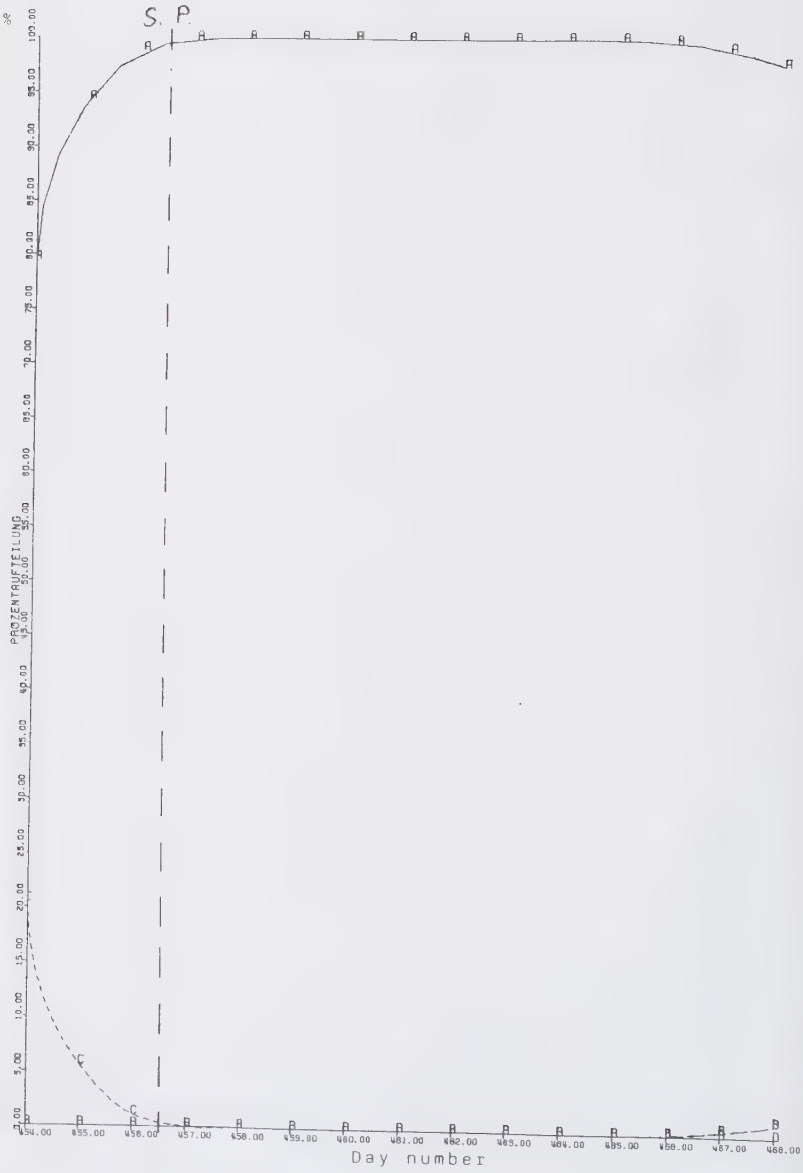


Fig.9b: Pellet intake by animal Nr.2 during Series VI A-D.

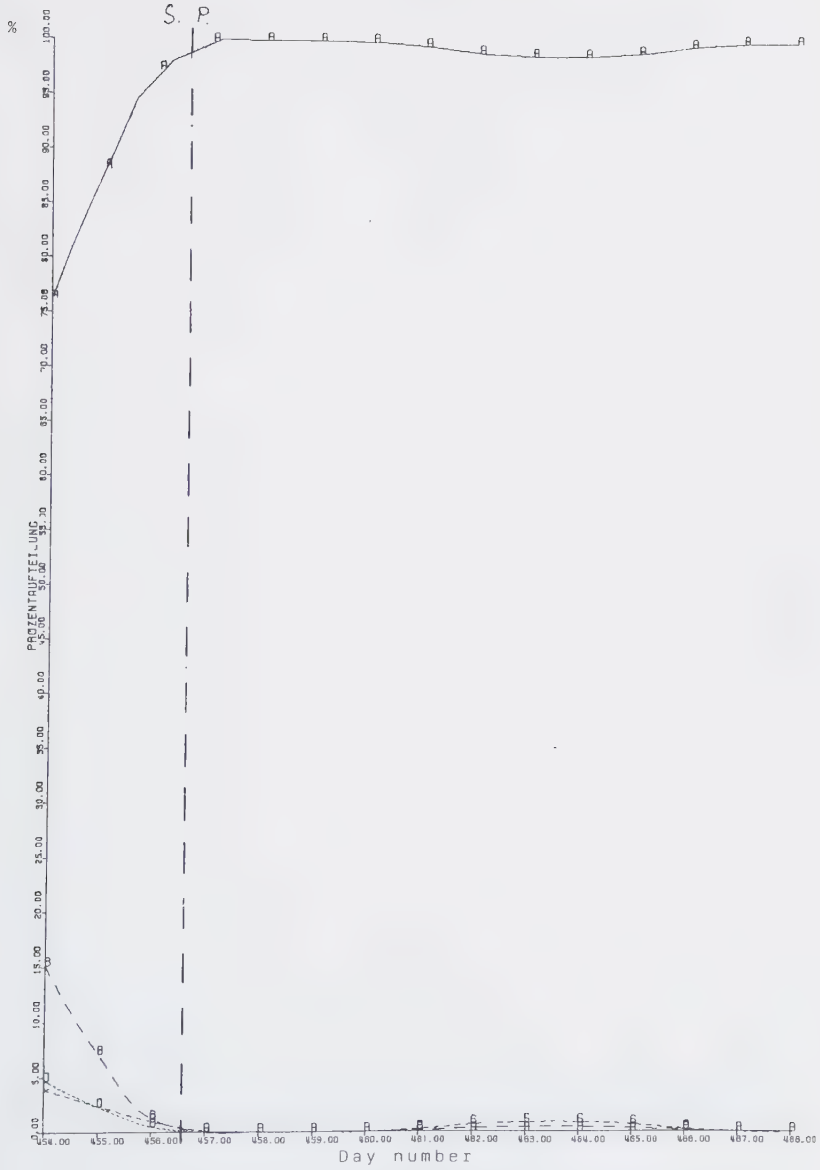


Fig.9c: Pellet intake by animal Nr.3 during Series VI A-D.

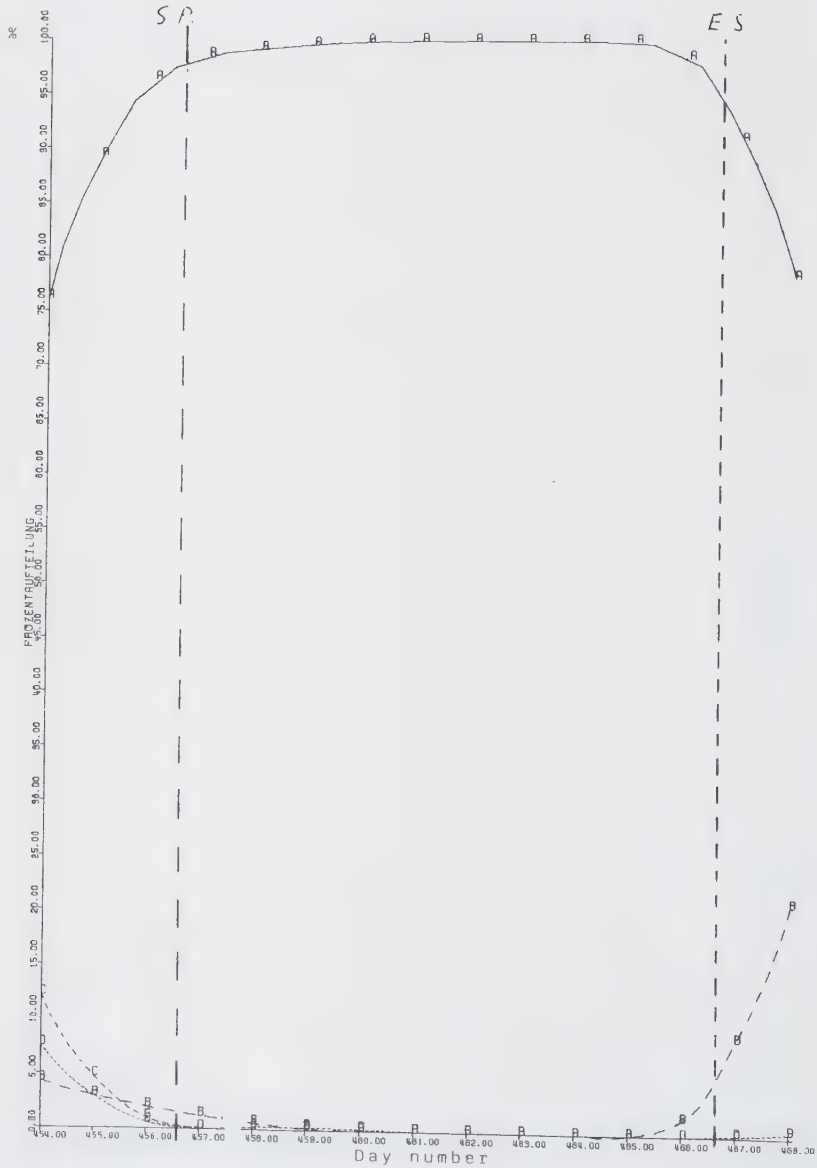


Fig.9d: Pellet intake by animal Nr.4 during Series VI A-D.

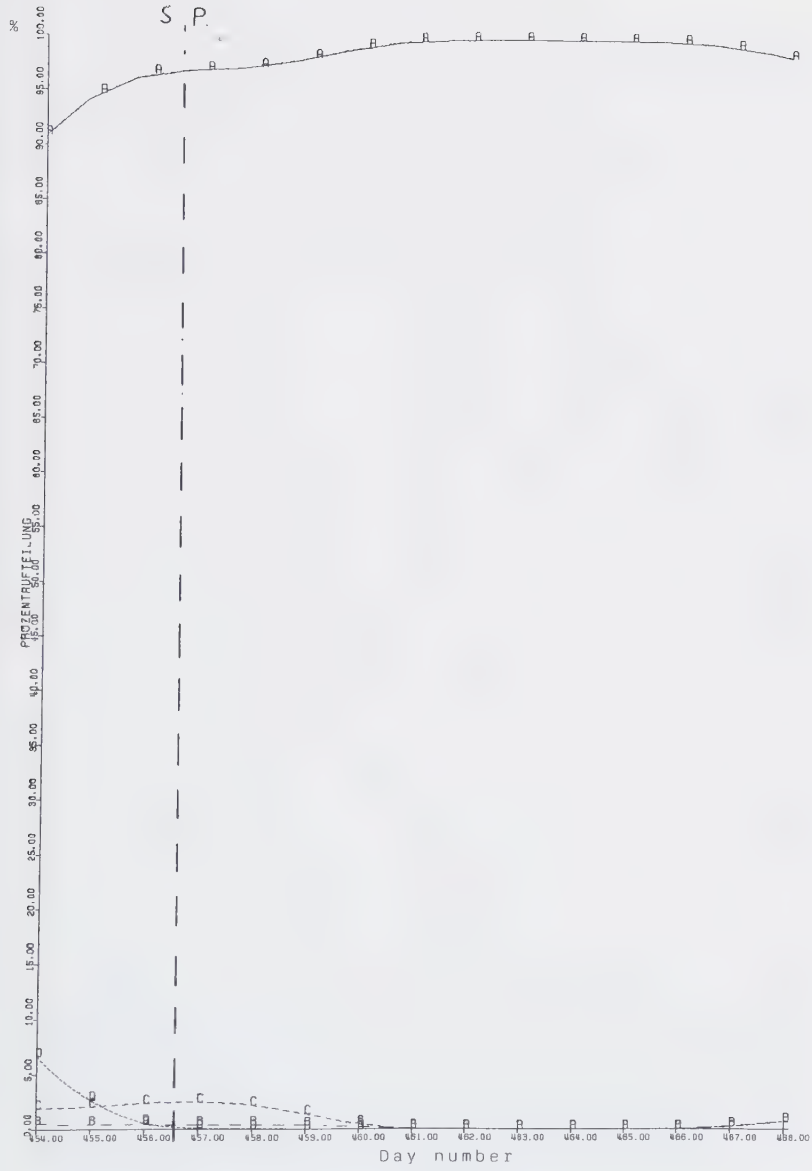


Fig.9e: Pellet intake by animal Nr.9 during Series VI A-D.

Fig.9f: Pellet intake by animal Nr.10 during Series VIA-D.

animals are grazers and not concentrate selectors. (A preference for the high-protein foods would have resulted in too high a protein intake).

The energy content within a food series did not vary greatly (ν = 3.0 or less), and therefore, the motivation to choose that food with the highest energy content was probably low. More importantly, the variation in NFE content within a food series was much higher (ν = 12.0 or more), and a high NFE content is strongly preferred. Since a strong negative correlation between NFE- and energy content exists (τ = -0.454; Z = 3.11, Kendall correlation coefficient), I suspect that a lower energy content is not really preferred by the animals, but rather the result of the animal's preference for NFE-rich foods.

Some animals (Nrs.1, 2, 4 and 9) significantly avoided foods with high straw content, others did not. On the other hand, all animals always completely consumed their hay ration, which was very high in fiber. The need for fibrous substances for a proper digestion is well known (CHURCH, 1972).

In Tab.9 the correlations are presented by food series. Only a few correlations diverge from expectation, i.e. differ from the generally valid correlations in Tab.8. In some cases these discrepances can be explained by the existence of autocorrelations between the food charac-

3.3.2 Food intake and daily input of nutrients

As expected, food intake varied from day to day, as shown in the "Total" column of Tab.18 in the Appendix. Over long periods however, standard deviation of mean food intake was rather low. For example male Nr.2 consumed an average 1520gr of pellets daily, with a standard deviation of σ=95.3. Naturally there were individual differences related to body weight and/or digestive capacities: the more corpulent male Nr.3 consumed nearly 300gr more each day than Nr.2, namely an average of 1810gr (σ=191.0).

In the females, a higher food intake related to pregnancy became evident about three months before kidding. This rise in food intake was slow, without a marked onset, and was largely masked by the daily variations in intake (see Figs.10 and 11). Just before kidding and few days afterwards, food intake showed a marked decline but again rose later on by about 30% (500gr) over the usual amount. The young antelopes began nibbling on hay at the age of five weeks, but substantial amounts of hay and pellets were not eaten before three months of age.

A drop in food intake was noted whenever a new food set was introduced (see again the "Total" column in Tab.18 of the Appendix). Intake appeared to return to normal values after one to five days; but because of daily variations, a more precise calculation was deemed meaningless.

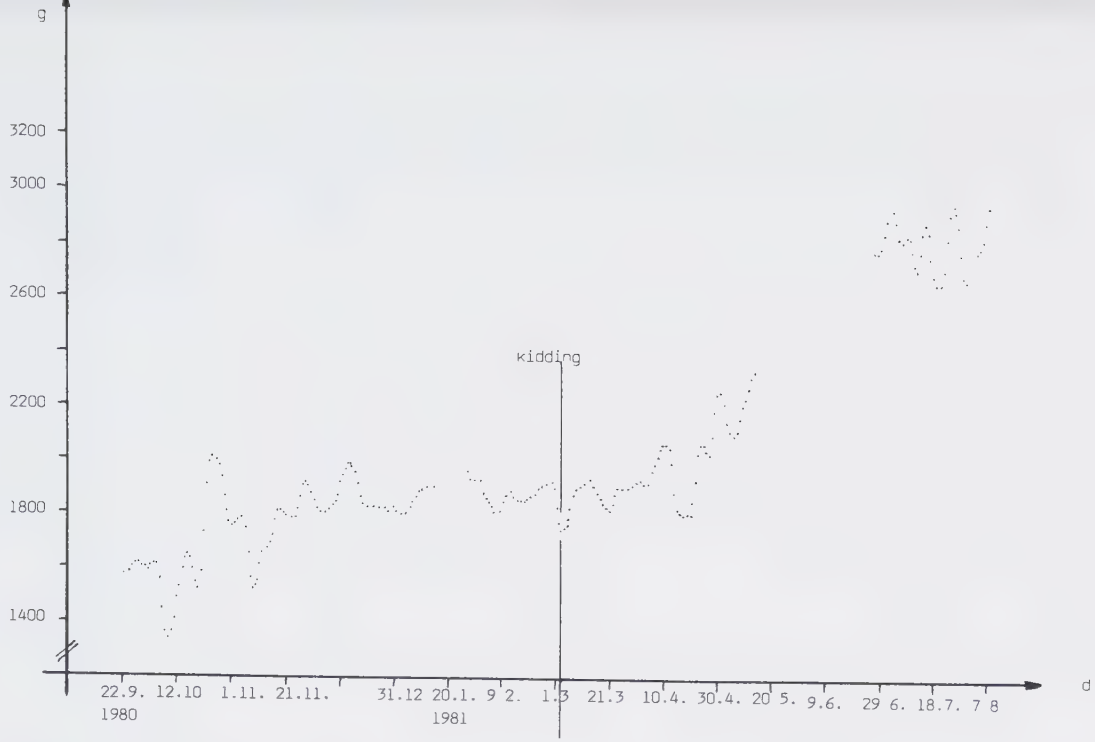


Fig 10· Daily food intake of animal Nr 1, before and after kidding
Data are drawn from smoothed values of total food intake

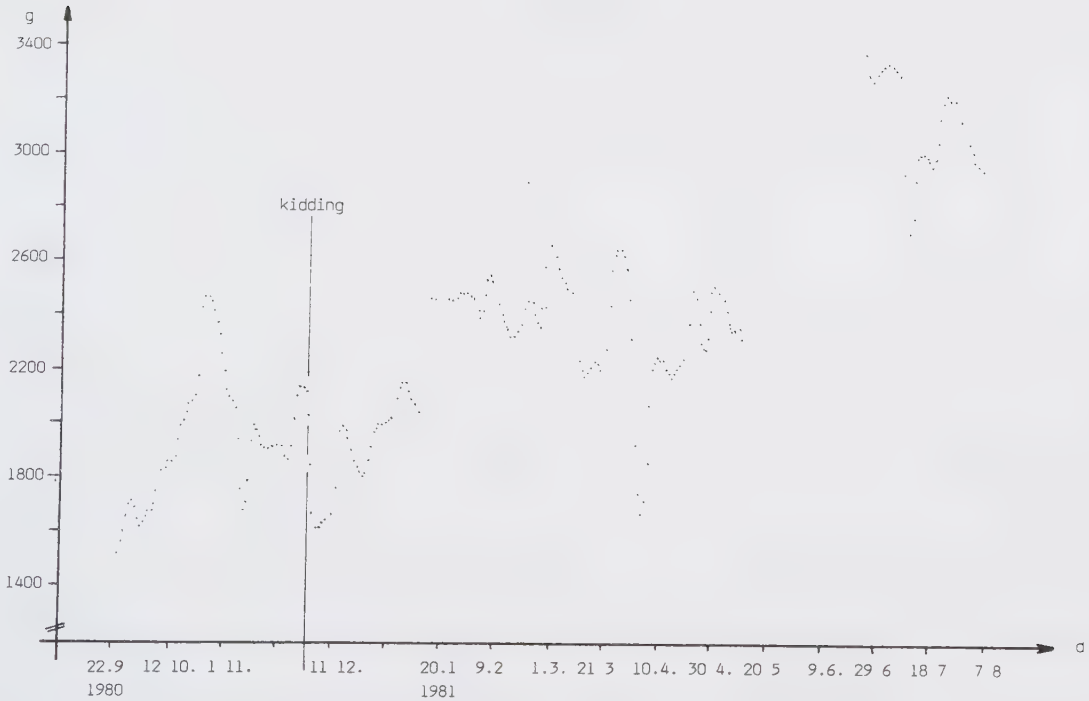


Fig 11 Daily food intake of animal Nr 10, before and after kidding
Data are drawn from smoothed values of total food intake

If the animals were offered only one pelleted food type (*ad lib.*) and hay, pellet intake did not drop markedly, even if the pellets were disliked (Fig.12). Contrary to this, the animals did not fully compensate with additional pellet intake if no hay was offered (Figs.13a-d). But this is true only of total food intake, and not with respect to utilizable nutrients. Without hay, the whole diet contains less fiber, and therefore, digestibility is increased. According to regression equations for digestibility and fiber content or nutrient detergent fiber content (NDF), the digestibility of the organic matter was approximately 85% for a pure pellet diet and about 70% for the diet consisting of pellets and hay. Comparing the nutrient intakes in Figs.13a-d, one notes that the intake of crude protein and gross energy are not changed as much as that of fiber, with or without hay. Intake of the other nutrients even remains constant.Thus, the higher digestibility of a pure pellet diet compensated for the small losses due to reduced food intake when no hay is available.

Considering deviations in nutrient intake during periods of stabilized food selection, it is interesting that crude protein intake generally fluctuated most, and fiber intake showed the greatest consistency: For animals Nr.2 and 3, the coefficients of variability for protein intake were v=11.5 and 19.1, respectively; for NFE, v=9.0 and

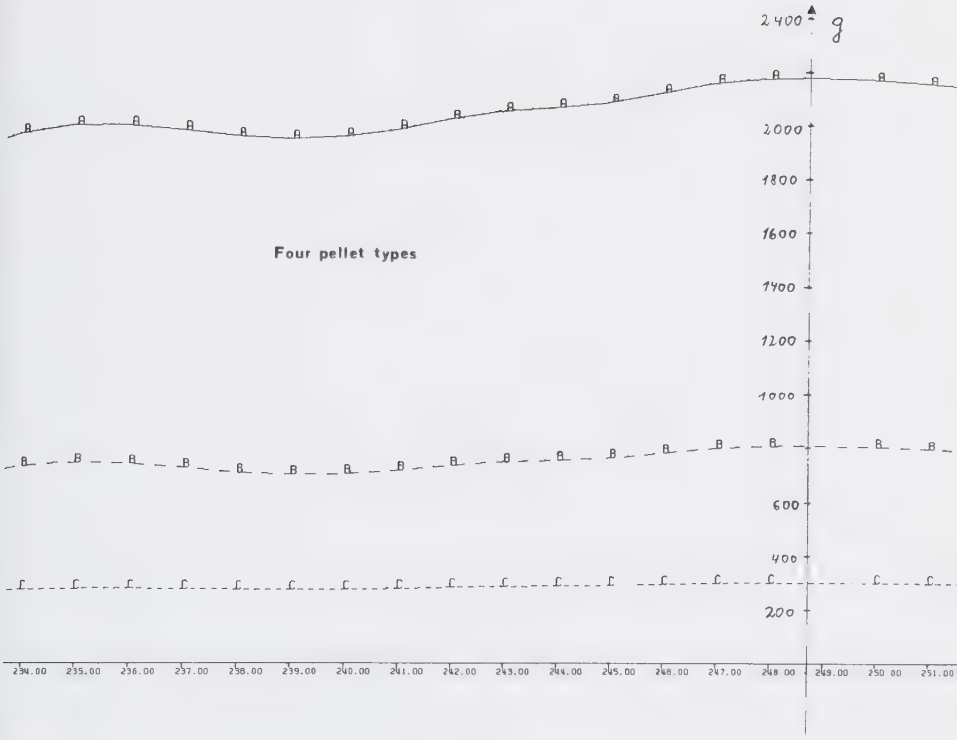
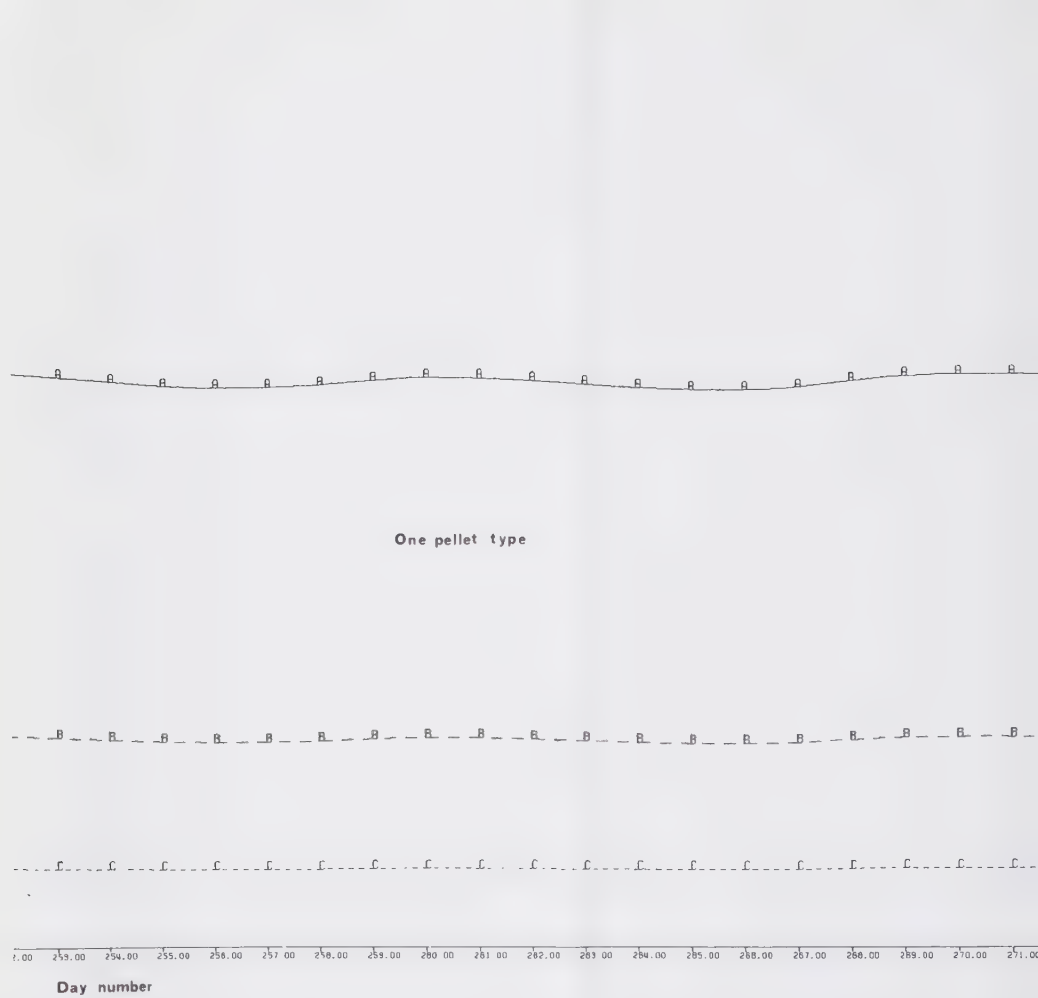


Fig.12: Total food intake when all four pellets (IV A-D) and hay are offered, and when only one food (IV C) plus hay is available. (Animal Nr.4).
A: total food intake
B: NFE intake
C: water intake (from food).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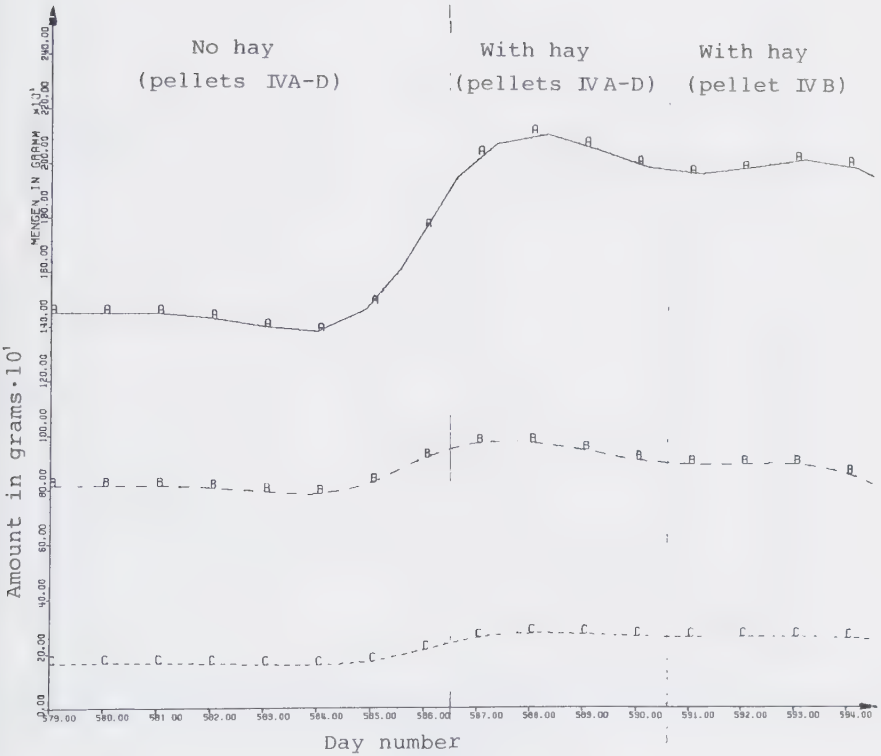

Fig.13: Total food intake and nutrient intake, when no hay is available, and when hay is offered. Foods: IVA-D; animal: Nr.3.

a) A: total food intake (fresh weight).
B: NFE intake
C: water intake (from food).

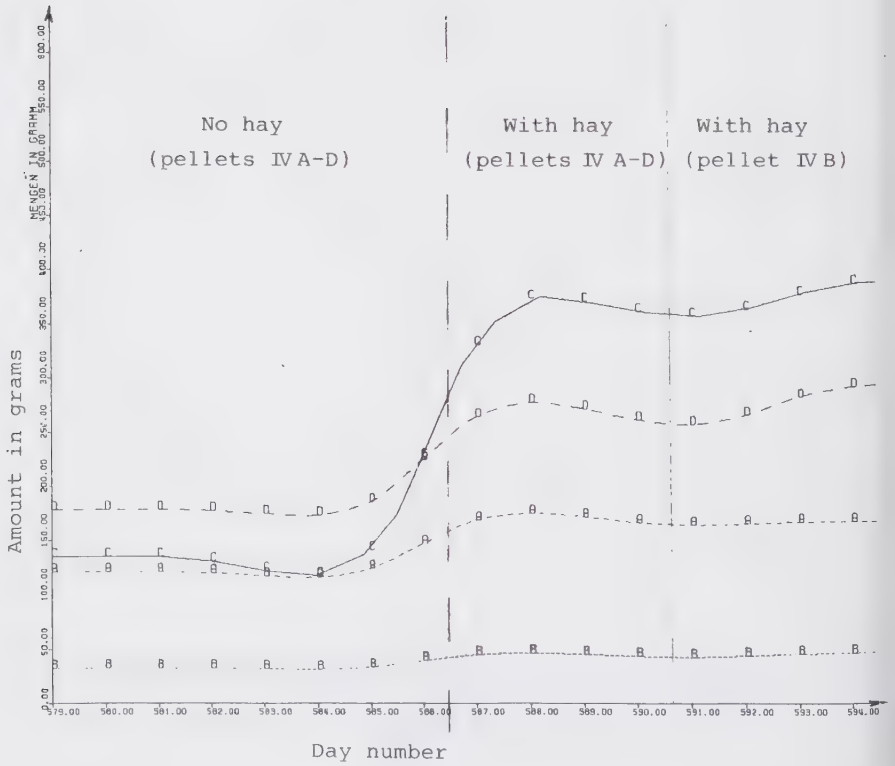

Fig.13b.

A: ash intake
B: fat intake
C: fiber intake
D: crude protein intake

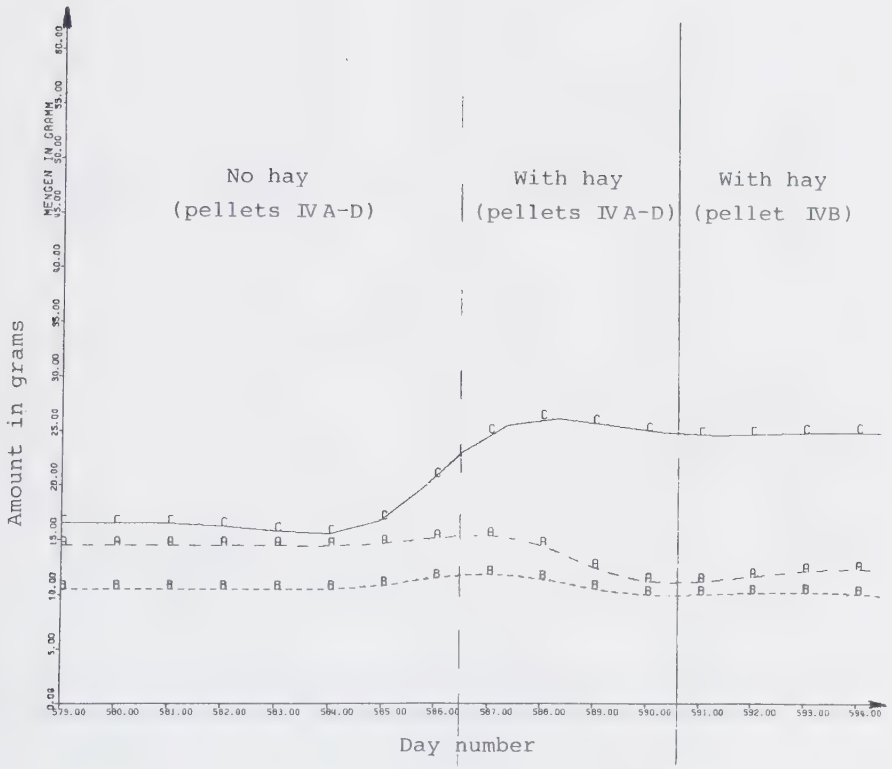

Fig. 13c.

A: intake of NaCl
B: intake of phosphorus
C: intake of calcium

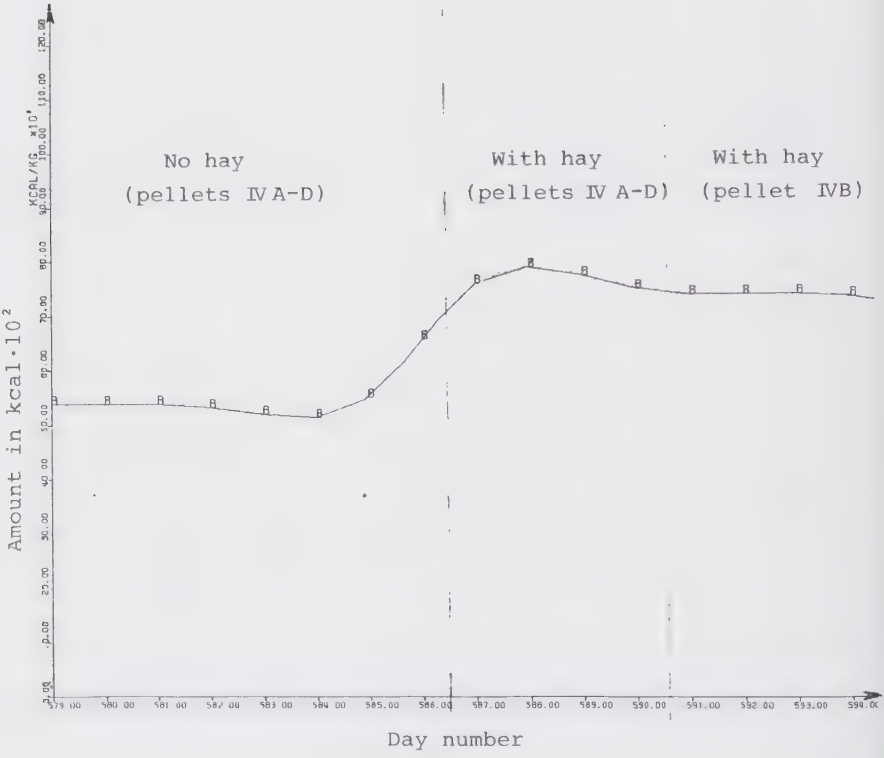

Fig.13d: Intake of gross energy.

13.8; for water, v=9.6 and 10.0; and for fiber, only 3.5 and 6.7. One might think that this is due to a lower variability in fiber content of the different foods; but since the coefficients of variability for total food intake were v=6.3 (animal Nr.2) and v=10.6 (animal Nr.3), v for fiber intake should then have reached the same values, even if fiber content were the same in all foods. Therefore, the lower values for fiber intake were indeed due to the animal's food selection.

The percentual daily consumption of crude fiber was higher just after the introduction of a new food, than at the end of a test; the consumption of NFE increased during the course of a test. This was due to reduced pellet intake after introduction of a new food set. Since the two tendencies were opposite, the percent crude protein input remained mor or less stable. But percent fiber and NFE intake did not stabilize even after an adaptation period when food choice stabilized (Fig.14). The explanation is quite simple: Although hay input was constant, total food intake was not, and as a result, percent input of nutrients changed with altering total food intake.

If one compares nutrient input between different animals and by those animals between the different test series as I have done in Figs.15a-c, several important points become apparent: first, inter-individual variation in

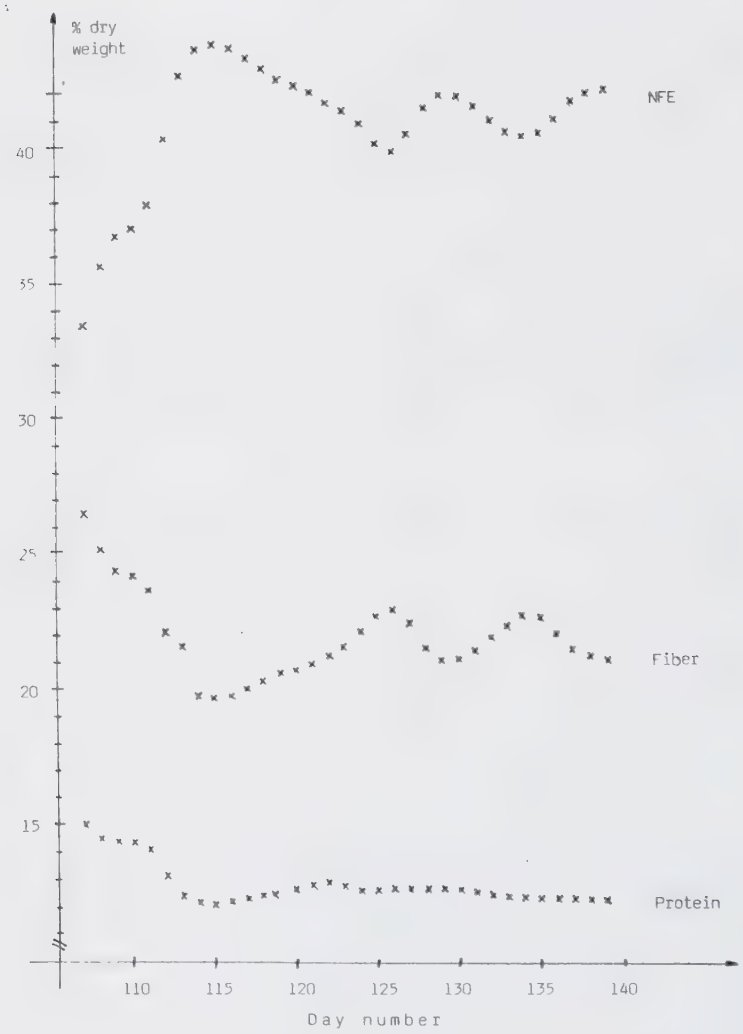

Fig.14· Typical changes in percentual nutrient intake during a test
Test begin at day 107
Food series II A-D, animal Nr 2

a)

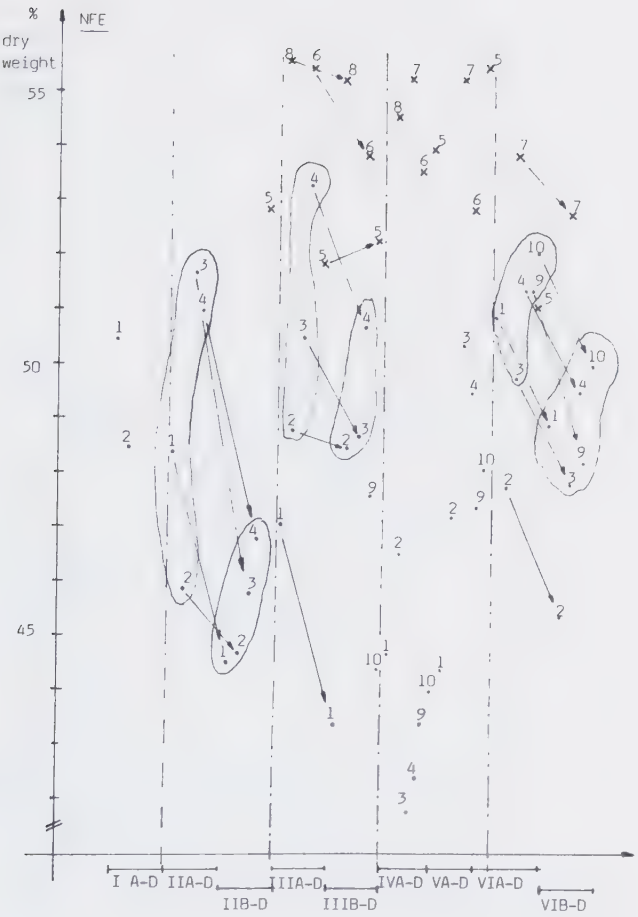

Fig.15: Mean values of nutrient intake in percent of total dry weight intake for a)NFE, b) fiber and c) protein.
"⟶": connect mean values for the same animal between 4- and 3-choice test situations.
• Arabian oryxes (animals 1-4, 9 and 10).
× : South African oryxes (animals 5-8).

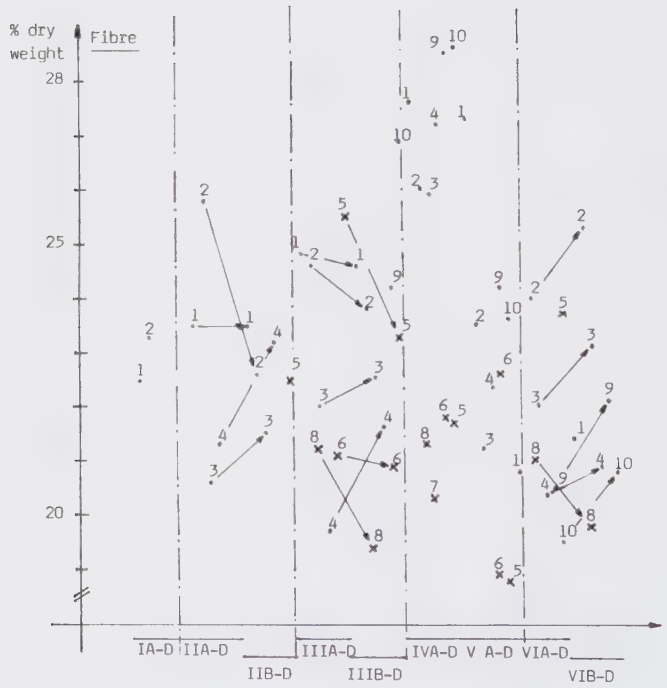

Fig.15b: Mean values of % fiber intake.

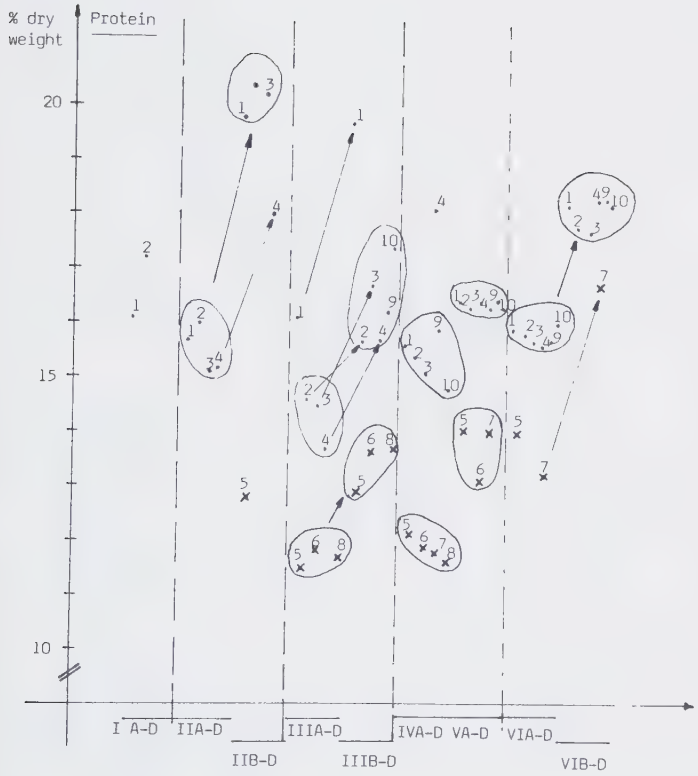

Fig.15c: Mean values of % protein intake.

the levels of nutrient intake was large. Secondly, those levels changed between tests, indicating that the animals were unable to maintain a constant nutrient intake when food quality altered, even though theoretically possible. But thirdly, the changes in levels of nutrient intake between two test series were most often in the same direction for the various individuals. And fourthly, the animals were obviously capable of maintaining levels of nutrient intake within their physiological limits (constraints), as evidenced by the absence of any health problems in the course of these experiments.

Looking more closely at the data in Fig. 15, the following generalizations may be made: If I omitted the most preferred food from a four-choice test situation, then in the three-choice test, the percent input of NFE was generally lower, and the mean fiber input and protein input were generally higher. When comparing the mean values of the two animal species, the South African oryxes showed higher values for NFE, and/or lower values for protein; for fiber input, the values of the two species were not separable.

When a female was near term or lactating, food, and as a consequence, nutrient intake was higher than usual; but there, no change in percent intake of the various nutrients was noted.

3.3.3 Comparison of actual and predicted diets

The hypothetical nutrient constraints, established by the method described in Section 3.2.5 (pp.43/44) and utilized for linear programming, are listed in Tab.11. A comparison of these values with intake values actually found (see Fig.15), shows that the hypothetical constraints indeed lie within the physiological constraints.

Character	Unit	Minimum	Maximum
NFE	% dry matter	42.2	50.6
Crude protein	% dry matter	14.0	20.0
Crude fiber	% dry matter	22.7	26.1
Ca:P	ratio	2.14	3.0
Protein:fiber	ratio	0.54	0.90
NFE:fiber	ratio	1.66	2.17
	For Arabian oryx:		
Food intake	g dry matter	900	2100
Gross energy	kcal	5980	-
	For South African oryx:		
Food intake	g dry matter	3500	7500
Gross energy	kcal	18470	-

Tab.11: Hypothetical nutrient constraints for Arabian oryx and South African oryx, used for linear programming.

As mentioned earlier, linear programming predicted diets on two levels - pellet intake and nutrient intake - for each of the four objective functions tested (maximum gross energy, maximum crude protein, maximum NFE, and minimum fiber). Each of the objectives was defined as a potential "strategy" of the animal's food selection, and the observed diets were compared with the various predicted diets by methods described in Section 3.2.5, to assess matching to a potential strategy.

On the level of pellet intake, the highest levels of correspondence between observed and predicted diets occurred when the objective functions were fiber minimization (40 out of 71 cases, in Tab.12) and NFE maximization (37 out of 71 cases, in Tab.12). With crude protein maximization as the objective function, best correspondence occurred in only 10 cases; and energy maximization never showed highest levels of correspondence.

By comparing the nutrient intake resulting from the pellet preferences, instead of the pellet intake itself, less clear and slightly different results were obtained (Tab.13). In 22 of 71 cases fiber minimization showed the smallest "distance" between predicted and observed diets; in 27 cases it was NFE maximization; in 18 cases, crude protein maximization; and in 13 cases, gross energy maximization.

Animal	I A-D	II A-D	II B-D	III A-D	III B-D	IV A-D	V A-D	VI A-D	VI B-D
1	NFE	NFE	P	NFE [P]	P/F [NFE]	NFE/F	F	F	NFE/F
2	NFE	NFE [P]	P	NFE	NFE/F	NFE/F [P]	F	F	NFE/F
3		NFE	NFE [P]	NFE	NFE/F	NFE/F [NFE/F]	F	F	NFE/F
4		NFE	NFE	NFE	NFE/F	P	F	F	NFE/F
9					NFE	NFE/F	F	F	NFE/F
10					NFE	NFE/F [NFE/F]	P	NFE	NFE/F
5		F		F	F	NFE	F	F	
6				F	F	NFE	F		
7						NFE	F	F F	P
8				F	F	NFE	NFE		

Tab.12: Objective functions of linear programs showing the smallest distances between theoretical and observed pellet intake (see text pp.45/46).
x/y: distances for both objectives equal, case counted twice.
[x]: smallest distance after switch of preference order, also counted twice.
P: protein, E: gross energy, F: fiber, NFE: nitrate free extracts

Animal	I A-D				II A-D				II B-D				III A-D				III B-D			
	P	E	NFE	F	P	E	NFE	F	P	E	NFE	F	P	E	NFE	F	P	E	NFE	F
1 (f)	8.6	7.1	1.0	3.1	7.5	6.8	1.0	1.0	1.4	1.0	7.7	5.9	4.2	1.0	1.2	2.9	1.0	4.2	8.9	11.3
													[1.0	1.8	6.0	7.7]	[1.0	2.8	7.3	9.7]
2 (m)	5.5	4.6	3.3	1.0	2.1	1.3	1.0	1.0	2.0	1.0	8.9	5.7	8.4	5.2	1.0	3.1	6.9	3.7	1.0	2.8
					[1.0	1.2	6.1	6.1]												
3 (m)	-	-	-	-	8.7	6.3	1.0	1.0	2.2	1.0	4.1	4.5	11.7	7.9	2.5	1.0	7.5	3.7	1.0	2.8
									[3.2	1.0	5.3	4.9]								
4 (f)	-	-	-	-	8.5	6.1	1.0	1.0	3.0	1.0	2.3	2.3	11.8	8.1	2.7	1.0	11.3	7.5	2.8	1.0
9 (f)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.3	2.0	1.0	3.4
10 (f)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0	2.7	4.3	6.8
5 (f)	-	-	-	-	1.0	1.4	2.3	4.3	-	-	-	-	1.2	1.0	2.5	4.4	3.7	1.0	2.8	4.3
6 (f)	-	-	-	-	-	-	-	-	-	-	-	-	5.3	3.5	1.0	2.9	2.9	1.6	1.0	3.1
7 (m)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8 (m)	-	-	-	-	-	-	-	-	-	-	-	-	2.7	2.2	1.0	2.9	4.9	3.7	1.0	2.1

Tab.13: Normalized "distances" between theoretical and observed nutrient intake, for each of the objective functions P, E, NFE and F.
[ ]: distances after a switch in food selection

Animal	IV A-D				V A-D				VI A-D				VI B-D			
	P	E	NFE	F	P	E	NFE	F	P	E	NFE	F	P	E	NFE	F
1 (f)	1.0	3.2	4.0	4.0	1.1	1.0	2.0	2.0	6.1	3.6	1.4	1.0	3.3	1.0	1.9	2.1
	[1.0	2.4	3.2	3.2]												
2 (m)	1.6	1.8	1.0	1.0	1.0	1.0	2.1	7.9	2.7	2.8	1.0	1.5	2.0	3.1	1.2	1.0
	[1.0	4.2	9.8	9.8]												
3 (m)	1.0	4.2	4.4	4.4	1.7	1.7	1.0	1.0	6.5	4.0	1.6	1.0	2.4	2.5	1.2	1.0
	[10.8	7.8	1.0	1.0]												
4 (f)	1.0	4.2	9.4	9.4	1.7	1.7	1.0	1.0	6.5	4.0	1.6	1.0	3.1	1.0	1.9	2.3
9 (f)	1.0	4.2	5.6	5.6	1.4	1.2	2.3	1.0	6.5	4.0	1.6	1.0	2.4	3.0	1.0	1.2
10 (f)	1.0	2.2	2.4	2.4	1,2	1.0	1.9	1.9	5.9	3.4	1.4	1.0	3.0	1.0	2.4	1.4
	[1.0	3.2	1.8	1.8]												
5 (f)	6.6	6.8	1.0	1.7	1.4	1.2	1.2	1.0	2.1	2.8	1.0	1.9	-	-	-	-
					[1.4	1.4	1.2	1.0]								
6 (f)	3.8	4.0	1.0	1.7	1.0	1.2	1.2	2.0	-	-	-	-	-	-	-	-
7 (m)	8.6	8.2	1.0	1.9	1.2	1.2	1.0	1.4	4.9	4.6	1.0	2.7	1.0	1.7	1.2	1.1
									[3.9	4.6	1.0	2.7]				
8 (m)	4.8	3.4	1.0	1.7	-	-	-	-	-	-	-	-	-	-	-	-

Tab.13 (cont'd).

Differences in strategy between the Arabian and South African species were neither consistent, nor frequent. From Tab.12, the South African animals appear to have selected pellets minimizing fiber content more often, or at least earlier on than the Arabian oryxes did. But based on total nutrient input (Tab.13), this was not confirmed. During Series IV, the Arabian animals appear to have maximized protein input, while the South African individuals clearly maximized NFE content; then during Series VI A-D, the Arabian oryxes placed more emphasis on fiber minimization (Tab.13).

A few additional points can be made from the data in Tab.13: In Food Series V A-D, the small differences between "distances" are conspicious. As mentioned earlier, the four foods of this series were most similar, relative to all other food sets. Then in food Series III, strategies of the various individuals were most inconsistent; in other series, a degree of conformity between animals is apparent.

Differences in the "distance-values" between the food series were more marked than those between the animals, as indicated by the mean square values of ANOVAs. For crude protein, e.g. the mean square value between the test series was 35.9, and that within the test series (i.e. between the animals), only 6.48. An F-test verified that these two values are significantly different

(F=5.52, F*=2.19, =0.05). The other mean square values between and within the test series were 14.21/3.16 for energy maximization, 11.70/4.46 for NFE maximization, and 12.04/5.40 for fiber minimization. Even the "distance values" of the test Series II A-D and VI A-D were significantly different from those of Series II B-D, respectively VI B-D.

By elimination of those cases where the difference between the two extreme mean values was less than 1.5, the remaining cases showed remarkable consistency of strategies followed. This was true for animals Nrs.3, 4, 6, 7 and 8, where the mean distances for NFE-maximization and fiber minimization were then clearly smaller than those for energy- or protein-maximization.

3.3.4 Digestibility of the diets

the results of the digestibility analyses using Cr_2O_3 were disappointing because of extreme variation in the values, even for samples from the same animal on the same diet. An example of these data is presented in Tab.14. This variation, which rendered the results useless, was probably due to several factors: Faecal samples may have taken too soon after trials where all

Animal	Digestibility (in%), Food series VI A-D			Digestibility (in %), Food series VI B-D		
1	52.5	47.3		40.6	54.4	
2	35.2	62.7		48.3	42.7	48.1
3	56.0			66.6		
4	52.9	60.5		55.2	55.4	
9	45.0	52.2		51.9	49.9	44.8
10	42.7	38.2	47.5	53.5	59.3	61.7

Tab.14: Digestibility of organic matter, calculated from faecal analyses. Each number in a row represents a sample from the same animal in chronical order.

pellet types were offered, affecting the results of the test with just one food type. But even then KANE *et al.* (1952) have demonstrated diurnal variations in the excretion of chromium oxide of about 10%; since I was unable to distinguish between faeces eliminated late in the evening and early in the morning, the samples were probably mixed, increasing variation in the results.

Nevertheless, an estimation of organic matter digestibility could still be made using neutral detergent fiber content (NDF), which is strongly correlated with digestibility (VAN SOEST, 1966; SALEWSKY, 1970). NDF content for all pelleted foods was between 23.1% and 13.3%, which represents an organic matter digestibility of 80%

to 90%. NDF content of diets consisting of hay and pellets was ca.33%, corresponding to an organic matter digestibility of about 70%.

3.3.5 Effects of tannins on food selection

Tannins are known to depress protein- and polysaccharide digestibility by complexing with them. Moreover, enzymes, complexed with tannins show a marked reduction in activity (SWAIN, 1979). Inspite of this, the results of investigations on tannin content and food preference are contradictory. HAWKINS (1955) found no correlation between tannins and preference in his study with cattle; WILKINS *et al.* (1953), however, found a strong negative correlation between tannin and preference of Lespedeza varieties by cattle.

In one last experimental series, tannin was added to the preferred food pellet IVD, which was offered together with the less preferred food, IVC, in a two-choice test. (Although pellet IVB was most preferred in the preceding test series, I was forced to substitute another preferred pellet for that, due to dwindling pellet stocks toward the end of my studies).

Inspite of the added tannin, no switching in food preference ocurred. Instead, total food intake was reduced in most cases, where tannin concentration was 1% or more.

An example of these data appears in Fig.16. Even the high concentration of 4% (presented only to non-pregnant animals) caused no switch in the pellet preference order - only a marked reduction in food intake.

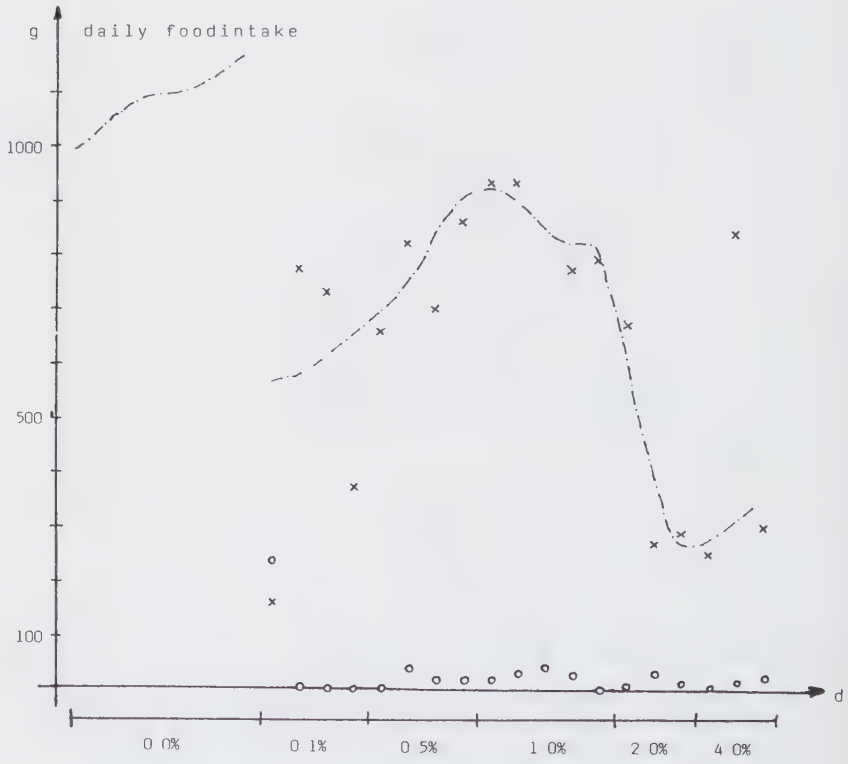

Fig.16: Intake of food IVD with tannin added and of food IVC, without tannin, in two-choice tests. The %-values on the time axis indicate the amount of tannin added during the corresponding period (in % fresh weight).
"-.-.-": Smoothed values of total intake (IVC + IVD).
× : Food IVD (with tannin).
O : Food IVC (without tannin).

3.3.6 Correction possibilities for imbalanced diets

Although most organisms are well equipped with reserves, long-lasting intake of an imbalanced diet would be fatal. Malnutrition could be avoided by correction of the imbalanced diet at subsequent meals. Theoretically, these corrections could be performed in one of two ways: 1) Correction at every subsequent meal (or other suitable intervals), independent of the magnitude of the deviation from optimum; or 2) correction only when a deviation from the optimum reaches a certain threshold value. This question can be answered by looking at the cumulative deviations from the optimum value. If a correction toward the optimum occurs at constant intervals, the animal has obviously applied the first method. If a correction only occurs after the sum of deviation has reached a margin value, the second method was more likely utilized. Under constant feeding conditions, the arithmetical mean daily intake of a nutrient may represent an optimum value. Under this assumption, cumulative deviations of crude fiber from the mean value are shown in Fig.17. It would appear that at least for crude fiber, the second correctional method may be applied. Whether this holds for all nutrients remains to be seen; a more careful analysis of this question was not the main object of this study and, although interesting, would expand the dissertation beyond page limitation.

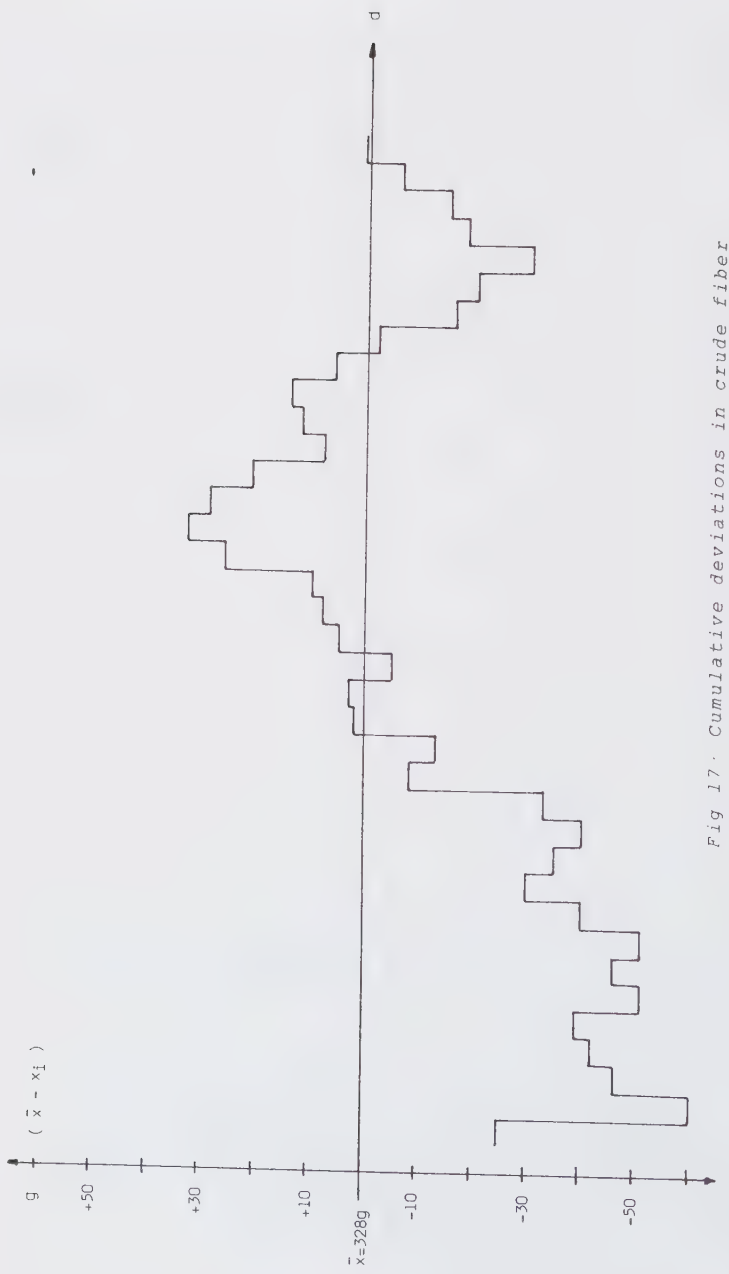

Fig 17. Cumulative deviations in crude fiber intake from the mean value, $\bar{x}$.

3.4 Discussion

3.4.1 Diet optimization and "nutritional wisdom"

Once again, this study has demonstrated that ruminants are capable of selecting the foods that compose their diet - even when those foods are as similar as the pellet types in my experiments. Selection was obviously deliberate, as evidenced by a) stabilization of diets after an introductory period, and b) re-establishment of preferences after a pellet-position switch between experiments.

Less easy to answer is the question concerning the aims of food selection. In the present experiments, most food characteristics were positively or negatively correlated with preference. The fact that these correlations were always in the same direction - for all animals and for all food series - indicates again, that the preferences and aversions did not result by chance. But autocorrelations between the food characteristics prevented any determination of those characteristics most likely to be involved in food selection. Particularly the autocorrelations between some food components and nutrient contents with preference orders masked whether the animals selected their diets according to nutrient content or food components.

To solve this problem, theoretical diets were calculated, with energy-, protein- and NFE-maximization and fiber minimization as objective functions. The comparisons of these theoretical diets with the observed diets revealed that the mean square values of the four "distances" within a test series were much lower than those between the test series (see also pp.118/119). This means the following: 1) The different animals react within a test series in a similar manner (low mean square values). 2) In terms of the four "strategies" the result of the animal's selection was different from sereis to series (compare also Tab.13, pp.116/117). It is concluded that food selection did not function basically on one of the four "strategies", since otherwise for all test series the "distances" to the same theoretical diet should be least. The argument that the animals could have altered their "strategy", e.g. during lactation, is plausible; but it is unreasonable that such switches take place simultaneously in all animals - males and females - as occurred during these tests (see Tab.13, Series IIA-D and IIB-D).

Other results indicate that food selection was probably based on food components and not directly on nutrient content: if nutrients were crucial for food selection, "least distances" should be the same whether comparing pellet intake or nutrient intake with the theoretical diets. This was not always the case.

When comparing pellet intake with the theoretical diets, in most cases least distances occurred with NFE maximization and fiber minimization. Hence, it follows that those food components which yielded high NFE- and low fiber content were most preferred by the animals. These were cereals, potato, molasses and pomace for NFE, and straw and grass for fiber. Indeed, the former components were significantly preferred by the animals, the later, significantly avoided.

Because the nutrient constraints used in calculation of the theoretical diets need not be identical with the true constraints, the deviations from optimality of the animal's diets are only relative in nature. Thus, no concrete statements about optimality of food selection can be made. However, I can conclude that an animal's diet was closer to the optimum in one respect, say maximization of NFE or minimization of fiber, than in another, say energy maximization.

Because of the value of the test animals, no experiments could be performed with extremely imbalanced diets. Thus, one part of the "nutritional wisdom" theory could not be examined. Nevertheless, one could regard as a nutritional "wise" behavior, the fact that all animals consumed hays rich in fiber ind addition to the pellets, which were poor in fiber. They did this, inspite of the facts that they clearly preferred the pellets over the

hays, and that pellets were presented *ad libitum*. This behavior led to a diet with a fiber content known to be optimal for cattle; and this indicates that factors other than palatability are probably involved in the decision-making process of food selection. Another indication of the animals' active search for a concrete amount of fiber was also observed: During the trials without hay, some animals began nibbling at their bedding material (straw). I suspect they would not have done this, if their food selection was only based on palatability, irrespective of physiological needs. With the exception of adult male Nr.7 (*Oryx beisa*), problems with digestion never occurred, and the animals always appeared in good nutritional health. Although it may seem trivial, this is a further indication that the animals were able to select their proper diets from the different food sets.

Highly pregnant and lactating females did not alter their food preferences in favor of foods richer in protein and/or energy, but increased their food intake. This may be adaptive in that no risky alteration of the rumen microorganisms occurs, when an animal continues to feed on familiar foods.

All of my experiments were performed with well-nourished animals and with high-quality foods; this undouptedly influenced their food selection, and some conclusions

are therefore restricted to those conditions. Nevertheless, the following findings will certainly hold in all situations: Both oryx species were able a) to distinguish between different complex foods (pellets), b) to select from those foods a constant diet, and c) to keep the diet within a range that was probably nearly optimal, certainly physiologically acceptable.

The question arises as to how applicable my experiments and results are to the field situation. Pelleted foods are certainly complex, with identical cues that originate from different components fusing into one, integrated cue. But natural foods also exhibit many cues, upon which the animal must base its decision to consume or to reject. The problem of differential recognition, therefore, is similar in both situations. Since the animals were able to select diets within reasonably narrow, hypothetical nutrient constraints from the complex pellets offered in my experiments, I can assume feedbacks between food selection and digestion. Whether that food selection was based on nutrient content or component characteristics could not be decided; nevertheless, the evidence supports the later, without disproving the former..

3.4.2 Accuracy of food selection

Clearly, the animals needed up to 14 days to adapt their

diets to a new food set, even when the new foods contained the same components. This supports the notion that food selection depends on gastrointestinal feedbacks (WESTOBY, 1974).

To ensure a properly functioning organism, appropriate food intake would be best at every meal. Obviously, the oryxes were not able to do that, and their food intake exhibited some deviations (see e.g. Tab.18a, Appendix). These deviations were large when a new food set was introduced, then became smaller with time, but never vanished. These "permanent" deviations were always smaller than 10v (v=Pearson's coefficient of variability) and neither constant nor species specific. The reason for their inconsistency is unclear, but differences in actual intake were certainly due to inaccuracies in food selection abilities.

3.5 Criticism and future studies

Looking back, the use of such valuable test animals proved to be a handicap; tests with foods of severe nutritional imbalance, which might have produced clearer results, were too risky to be allowed. Nor were the experimental conditions available in the zoo stable enough to eliminate all sources of error. Nevertheless, I am still convinced that such investigations should not be conducted using metabolic crates (because of animal

stress and its side effects), and that food selection capabilities must also be examined in wild species due to domestication effects.

My investigations did not succeed in separating nutritive and non-nutritive factors in food selection; but they did indicate that non-nutritive aspects may play the greater role in selection, at least when the foods are of well-balanced composition. And I did succeed in demonstrating that linear programs could be utilized to investigate the aims of food selection. For future studies on wild species, more accurate values for the nutrient constraints would be desirable, as well as more powerful methods of comparing "distances" between the theoretical and observed diets.

3.6 Summary

Four-choice preference tests with pelleted foods showed that in most cases, *Oryx leucoryx* and *Oryx beisa* highly preferred one or two pellet types over the others. The preference patterns were astonishing similar between different animals, and between the two test species.

These experiments were performed on well-nourished animals using high-quality foods. Under these conditions, the foods preferred by all animals showed significantly higher NFE content and lower concentrations of fiber,

gross energy and protein, than the other foods. With respect to the components of the foods, preferred pellets contained significantly higher concentrations of cereals and potato, but less soybean- or rape solv-extd, and also less straw.

The negative correlation between protein content and preference could be explained by strong negative autocorrelation with cereals and preference for those. Correspondingly, the negative correlation between gross energy content and preference could be explained by the negative autocorrelation between gross energy and NFE content, NFE being highly preferred. Most other pellet components also showed correlations between preference and their concentration, but less clearly and less consistently.

As shown by Kendall-rank-correlation tests, many food characteristics were correlated with each other. Because of those autocorrelations, separation of characteristics which really did contribute to food selection from those which were only correlated with the former, was not possible.

In a further attempt to estimate the contribution nutritive food characteristics make in the food selection process, theoretical diets were calculated with the aid of linear programs. The resulting theoretical diets were compared with those observed in the experiments. From

these comparisons, I concluded that food components influence food selection more than nutritive characteristics under the given conditions. However, I can not eliminate nutritive characteristics as a factor in food sesection if either the foods show greater nutritional imbalances or the animals themselves are malnurished. Because of their value, I could not perform such experiments on the present test animals.

3.6 Zusammenfassung

In Vierfach-Wahlversuchen mit pelletiertem Futter zeigten die Versuchstiere der Arten *Oryx leucoryx* und *Oryx beisa* eindeutige Präferenzen. In den meisten Fällen wurden ein oder zwei Futtertypen stark bevorzugt, während die übrigen Futter kaum gefressen wurden. Die Futterpräferenzen wiesen erstaunlich geringe interspezifische- und intraspezifische Unterschiede auf. Die vorliegenden Versuche wurden mit Tieren in gutem Ernährungszustand und mit bedarfsdeckendem Futterangebot durchgeführt. Unter diesen Bedingungen wiesen die bevorzugten Futter bei allen Tieren einen höheren NFE-Gehalt, jedoch einen niedrigeren Rohfaser-, Energie- und Protein-Gehalt auf, als die unbeliebten Futter. Bezüglich der Futterkomponenten enthielten die bevorzugten Futter signifikant höhere Anteile an Getreide und Kartoffelmehl, jedoch weniger Soja- und Raps-Extraktionsschrot, sowie weniger Strohmehl.

Die negative Korrelation zwischen Präferenz und Proteingehalt liess sich durch die starke negative Autolorrelation mit dem Getreideanteil im Futter und dessen Präferenz erklären. Entsprechend erklärt die negative Autokorrelation zwischen Energie- und NFE-Gehalt die negative Korrelation zwischen Energiegehalt und Futterpräferenz. Auch die meisten anderen Pellet Komponenten wiesen Korrelationen zwischen Präferenz und Konzentration auf, wenn auch nicht so eindeutig und ausnahmslos.

Wie Kendall-Rang-Korrelationsstests bewiesen, sind einige Futtercharakteristika miteinander korreliert. Wegen der vielen Variablen genügte das Datenmaterial nicht, diejenigen Charakteristika, welche wirklich die Futterwahl bestimmen, varianzanalytisch von denjenigen zu trennen, welche nur mittels ihrer Korrelationen einen scheinbaren Beitrag zur Futterwahl leisten.

In einem weiteren Versuch, die Bedeutung der nutritiven Eigenschaften eines Futters für die Futterwahl zu ermitteln, wurden theoretische Diäten errechnet. Dies geschah mit Hilfe von Linearprogrammen. Die daraus resultierenden theoretischen Diäten wurden mit den aus den Experimenten erhaltenen Diäten verglichen. Dabei zeigte sich, dass unter den gegebenen Bedingungen die Futterkomponenten die Futterwahl eindeutig stärker beeinflussen als die nutritiven Eigenschaften. Es ist jedoch nicht auszuschliessen, dass bei Futtermitteln, mit starken

nutritiven Imbalancen, die nutritiven Eigenschaften ein stärkeres Gewicht bei der Futterwahl haben werden. Wegen der wertvollen Tiere, konnten solche Versuche jedoch nicht durchgeführt werden.

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6. Appendicies

Component	I A	I B	I C	I D	II A	II B	II C	II D	III A	III B	III C	III D
Barley	6.0	4.0	1.0	6.0	5.0	3.0	1.0	4.0	7.0	5.0	1.0	3.0
Corn	18.0	6.0	4.0	3.0	20.0	8.0	8.0	6.0	20.0	8.0	7.0	8.0
Rye	13.0	10.0	2.0	1.0	15.0	11.0	1.0	1.0	14.0	12.0	1.0	1.0
Oats	6.0	1.0	4.0	3.0	4.0	1.0	2.0	2.0	4.0	2.0	5.0	2.0
Wheat	10.0	14.0	3.0	2.0	12.0	14.0	6.0	5.0	12.0	16.0	2.0	7.0
Linseed,solv-extd	0.5	3.0	6.0	10.0	-	2.0	3.0	7.0	-	1.0	4.0	9.0
Coconut,solv-extd	1.0	9.0	11.0	15.0	1.0	8.0	13.0	14.0	1.0	5.0	12.0	7.0
Rape, solv-extd	0.5	3.0	7.0	10.0	-	2.0	7.0	8.0	-	3.0	8.0	9.0
Soybean, solv-extd	0.5	8.0	14.0	20.0	-	6.0	12.0	16.0	-	5.0	14.0	20.0
Wheat, ground	0.5	4.0	1.0	2.0	-	3.0	2.0	1.0	2.0	3.0	2.0	2.0
Mixed grass, ground	10.0	14.0	23.0	11.0	8.0	12.0	17.0	10.0	6.0	6.0	14.0	6.0
Wheat bran	1.0	0.5	1.0	5.0	2.0	-	1.0	1.0	-	-	2.0	5.0
Potato, ground	8.0	9.5	1.0	2.0	9.0	12.0	2.0	3.0	8.0	12.0	2.0	1.0
Molasses	4.0	4.0	3.0	4.0	4.0	3.0	2.0	4.0	5.0	5.0	2.0	4.0
Rice, ground	2.0	0.5	1.0	0.5	2.0	-	2.0	2.0	2.0	-	3.0	5.0
Straw, ground	-	-	-	-	-	-	-	-	3.0	4.0	2.0	-
Pomace	10.0	0.5	5.0	1.0	8.0	3.0	6.0	4.0	6.0	1.0	6.0	1.0
Beet pulp	1.0	1.0	5.0	1.0	2.0	4.0	7.0	4.0	2.0	4.0	5.0	2.0
Elements & vit.	8.0	8.0	8.0	8.0	8.0	8.0	8.0	8.0	8.0	8.0	8.0	8.0

Tab.15: Food components of the pellets in % of fresh weight.

Component	IV A	IV B	IV C	IV D	V A	V B	V C	V D	VI A	VI B	VI C	VI D
Barley	9.0	6.0	10.0	4.0	5.7	6.0	5.8	5.8	8.0	8.2	8.0	1.0
Corn	20.0	20.0	10.0	6.0	17.0	18.0	17.3	17.3	11.0	3.0	11.0	1.0
Rye	10.0	16.0	5.0	12.0	14.2	15.0	14.4	14.5	11.0	3.0	11.0	1.0
Soybean, solv-extd	0.5	4.0	14.0	2.0	3.8	4.0	3.8	3.8	2.0	2.0	7.0	1.9
Rape, solv-extd	0.5	3.0	12.0	10.0	1.9	2.0	1.9	1.9	5.0	5.0	5.0	4.8
Wheat, ground	4.0	6.0	5.0	4.0	5.7	6.0	5.8	5.8	15.0	2.0	11.0	1.9
Potato, ground	8.0	12.0	1.0	4.0	10.6	11.2	10.8	10.8	15.0	2.0	15.0	1.9
Straw, ground	16.0	2.0	12.0	5.0	6.6	4.0	3.8	7.7	2.8	27.6	2.8	17.4
Pomace	8.0	6.0	4.0	5.0	5.7	6.0	5.8	5.8	6.0	2.0	6.0	1.9
Mixed grass,ground	14.0	12.0	17.0	17.0	10.8	11.5	11.1	11.1	13.0	3.0	11.0	2.9
Molasses	2.0	5.0	2.0	5.0	3.8	4.0	3.8	3.8	3.0	3.0	3.0	2.9
Elements & vit.	8.0	8.0	8.0	8.0	7.5	8.0	7.7	7.7	8.0	8.0	8.0	8.0
Potato - starch	-	-	-	-	2.8	-	3.8	-	-	22.5	-	36.3
Soybean protein	-	-	-	-	3.8	4.0	3.8	3.8	-	8.4	1.0	17.1
Chromium oxide	-	-	-	-	0.28	0.30	0.29	0.29	0.17	0.17	0.17	0.17

Tab.15 (cont'd).

Nutrient	I A	IB	IC	ID	II A	II B	II C	II D	III A	III B	III C	III D
Water	11.0	11.0	10.0	11.0	12.5	13.0	11.0	12.5	13.0	13.0	11.0	12.5
Crude protein	11.3	17.3	21.4	25.2	10.7	14.5	18.7	21.5	9.9	12.3	18.2	21.5
Crude fiber	8.9	7.6	13.1	10.1	7.3	7.7	12.6	9.7	7.6	7.0	12.3	8.7
Fat	3.2	2.7	3.7	3.3	2.5	2.1	2.7	2.8	2.4	2.1	2.7	3.2
Ash	5.7	6.1	6.9	6.8	9.2	8.3	9.2	8.4	8.2	8.4	8.1	8.1
NFE	59.9	55.3	44.9	43.6	57.8	54.4	45.8	45.1	58.9	57.2	47.7	46.0
Gross energy	3875	3915	4075	4055	3610	3665	3840	3840	3615	3625	3875	3870
Ca	0.80	0.44	0.76	0.52	1.26	1.08	1.10	1.16	1.04	1.12	1.04	1.18
P	0.53	0.60	0.70	0.79	0.87	0.87	0.90	0.87	0.82	0.77	0.79	0.90
NaCl	0.40	0.40	0.47	0.35	0.82	1.05	0.95	0.95	0.70	0.80	0.99	0.99

Tab.16: Nutrient content of the pellets in % of fresh weight.

Nutrient	IV A	IV B	IV C	IV D	V A	V B	V C	V D	VI A	VI B	VI C	VI D
Water	10.5	11.0	12.0	12.0	13.0	13.0	13.0	13.0	13.0	12.0	12.5	9.0
Crude protein	10.0	12.0	17.2	19.0	13.6	14.5	14.1	14.3	13.0	14.3	17.5	20.2
Crude fiber	13.6	8.7	12.6	11.4	8.4	7.8	7.8	8.7	7.8	12.7	8.3	8.8
NDF	23.1	15.0	25.0	17.8	14.7	13.7	13.3	15.9	15.3	21.5	14.9	14.6
Fat	2.1	2.3	2.2	2.0	1.8	1.9	1.9	2.0	2.3	1.0	1.1	0.8
Ash	10.9	9.1	10.0	9.7	8.6	9.0	8.5	9.2	9.2	8.8	8.7	8.7
NFE	52.9	56.9	46.0	45.9	54.6	53.8	54.7	52.8	54.7	51.2	51.9	52.6
Gross energy	3630	3695	3715	3735	3630	3625	3640	3625	3615	3655	3665	3845
Ca	1.14	1.02	1.12	1.02	0.96	1.06	0.98	1.04	1.01	0.79	0.92	0.81
P	0.83	0.77	0.74	0.87	0.64	0.71	0.70	0.78	0.75	0.64	0.67	0.68
NaCl	0.76	0.95	0.95	0.95	1.11	1.17	0.99	0.99	1.21	1.19	1.16	1.22

Tab.16 (cont'd).

a)

Day number	Foods consumed(in gramms)					
	Alfalfa	A	B	C	D	Total
107	900	0	0	0	165	1065
108	900	305	10	0	20	1235
109	900	95	20	0	280	1295
110	900	10	15	345	0	1270
111	900	320	10	0	0	1230
112	900	400	0	70	0	1370
113	900	800	0	60	0	1760
114	900	800	0	0	0	1700
115	900	710	0	0	0	1610
116	900	850	0	0	0	1750
117	900	345	0	5	0	1250
118	900	670	0	0	100	1670
119	900	625	0	0	10	1535
120	900	625	0	0	15	1540
121	900	235	0	0	240	1375
122	900	660	0	0	0	1560

Tab.17: Example of data processing at the level of pellet intake.
a) raw data on foods consumed (in g);
b) Smoothed data for pellet intake (in g and % fresh weight).

Day number	Pellets consumed (in g and %; smoothed values) A	B	C	D	Total
107	2 1.0	3 1.9	0 0.0	161 97.1	165
108	54 34.3	8 5.1	0 0.0	96 60.6	158
109	104 62.3	11 6.5	6 3.8	46 27.3	167
110	170 78.5	12 5.3	23 10.7	12 5.5	217
111	289 85.9	9 2.8	38 11.3	0 0.0	336
112	485 91.3	4 0.8	42 7.9	0 0.0	532
113	673 94.7	1 0.1	37 5.2	0 0.0	711
114	754 97.3	0 0.0	21 2.7	0 0.0	776
115	761 99.3	0 0.0	5 0.7	5 0.0	766
116	734 99.9	0 0.0	0 0.0	0 0.1	734
117	687 99.5	0 0.0	0 0.0	4 0.5	691
118	649 98.7	0 0.0	0 0.0	9 1.3	657
119	632 98.2	0 0.0	0 0.0	12 1.8	644
120	619 98.0	0 0.0	0 0.0	12 2.0	632
121	595 98.3	0 0.0	0 0.0	10 1.7	606
122	569 98.9	1 0.2	0 0.0	5 0.9	576

Tab.17b.

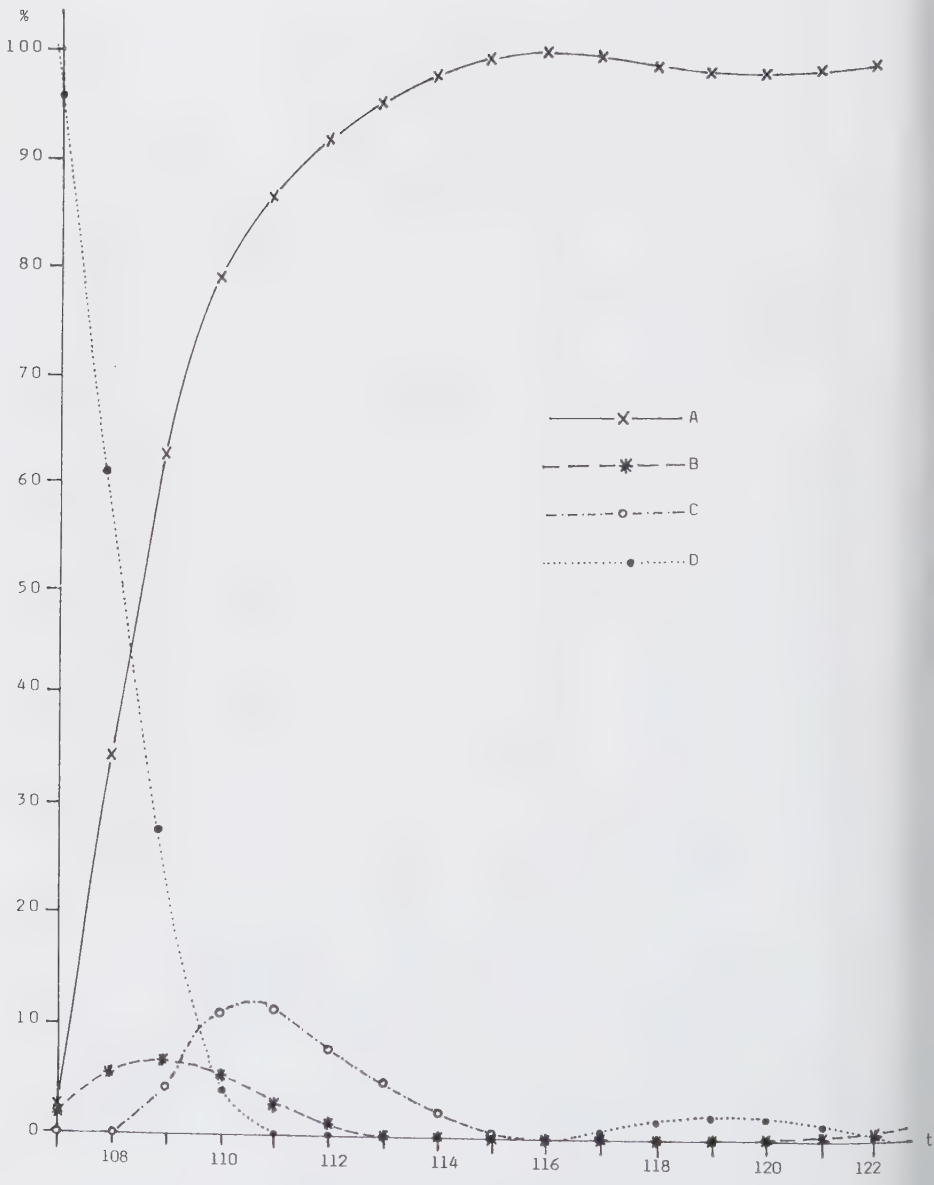

Fig.18: Graph of the smoothed values in Tab.17b.

a)

Day number	Daily nutrient intake (in gramms; energy in kcal)										
	Water	Protein	Fiber	Fat	Ash	NFE	Total	Ca	P	NaCl	Energy
107	156	161	284	23	85	355	1065	15	3	2	3987
108	178	162	296	26	99	474	1235	16	5	3	4565
109	185	198	303	30	104	475	1295	17	5	4	4848
110	176	192	314	28	102	458	1270	16	5	4	4777
111	178	159	295	26	99	473	1230	16	5	3	4542
112	195	178	309	29	110	548	1370	17	6	4	5066
113	246	216	338	39	142	779	1760	22	9	7	6473
114	239	205	331	37	138	750	1700	21	8	6	6240
115	227	196	324	35	130	697	1610	20	8	6	5915
116	246	210	335	38	142	780	1750	21	9	7	6421
117	180	161	297	26	101	485	1250	16	5	3	4615
118	235	214	330	37	135	720	1670	21	8	6	6157
119	218	190	318	33	124	652	1535	19	7	5	5646
120	218	191	319	33	124	654	1540	19	7	5	5666
121	196	201	309	31	111	528	1375	18	6	5	5127
122	221	191	320	34	126	668	1560	19	7	5	5734

Tab.18: Example of data processing at the level of nutrient intake: a) raw values and b) smoothed values from the proximate analyses (in g. and kcal.), and c) intake in % of total fresh weight (smoothed values). Sampling period: 13. July - 28 July, 1980. Food series: IIIA-D. Animal: Nr.2.

Day number	Daily nutrient intake (in g; energy in kcal; smoothed values)										
	Water	Protein	Fiber	Fat	Ash	NFE	Total	Ca	P	NaCl	Energy
107	159	162	286	23	87	359	1076	15	3	2	4059
108	168	170	294	25	95	416	1169	15	4	3	4405
109	174	177	300	27	99	450	1227	16	5	3	4620
110	178	182	304	27	102	465	1257	16	5	4	4736
111	185	185	309	29	106	497	1311	17	5	4	4922
112	202	189	316	31	116	577	1430	18	6	5	5316
113	222	195	323	34	127	670	1572	19	7	5	5791
114	233	201	328	36	134	721	1653	20	8	6	6085
115	236	203	330	37	136	733	1674	21	8	6	6177
116	235	203	329	37	135	728	1668	21	8	6	6156
117	231	201	327	36	133	709	1636	20	8	6	6037
118	225	197	323	34	128	681	1588	20	7	5	5855
119	220	194	320	33	125	660	1552	19	7	5	5707
120	217	193	318	33	123	648	1532	19	7	5	5624
121	213	193	316	32	121	633	1508	19	7	5	5524
122	209	191	314	32	119	616	1480	19	7	5	5416

Tab.18b.

Day number	Daily nutirent intake (in %; smoothed values)								
	Water	Protein	Fibre	Fat	Ash	NFE	Ca	P	NaCl
107	14.8	15.0	26.6	2.1	8.1	33.4	1.4	0.3	0.2
108	14.4	14.5	25.2	2.2	8.1	35.6	1.3	0.4	0.2
109	14.2	14.4	24.4	2.2	8.1	36.7	1.3	0.4	0.3
110	14.2	14.4	24.2	2.2	8.1	37.0	1.3	0.4	0.3
111	14.1	14.1	23.6	2.2	8.1	37.9	1.3	0.4	0.3
112	14.1	13.2	22.1	2.2	8.1	40.3	1.2	0.4	0.3
113	14.1	12.4	20.6	2.2	8.1	42.7	1.2	0.5	0.3
114	14.1	12.2	19.8	2.2	8.1	43.6	1.2	0.5	0.4
115	14.1	12.1	19.7	2.2	8.1	43.8	1.2	0.5	0.4
116	14.1	12.2	19.8	2.2	8.1	43.6	1.2	0.5	0.4
117	14.1	12.3	20.0	2.2	8.1	43.3	1.2	0.5	0.4
118	14.2	12.4	20.3	2.2	8.1	42.9	1.2	0.5	0.3
119	14.2	12.5	20.6	2.1	8.1	42.5	1.2	0.5	0.3
120	14.2	12.6	20.7	2.1	8.0	42.3	1.2	0.5	0.3
121	14.1	12.8	20.9	2.2	8.0	42.0	1.2	0.4	0.3
122	14.2	12.9	21.2	2.2	8.0	41.6	1.2	0.4	0.3

Tab.18c.

Fig.19: Graph of the smoothed values in Tab.18c.

Curriculum vitae

Rusterholz, Moritz Stephan

Born on December, 30th 1949 in Zurich, Switzerland.

I went to primary school in Regensberg and Zurich, Switzerland. Afterwards, I attended a private secondary school (high school) in Zurich, with emphasis on mathematics and natural science. From autumn 1971 to spring 1973, I studied mechanical engineering at the Federal Institute of Technology (ETH) in Zurich. In autumn 1973, I began my biology studies at the university of Zurich and obtained my Master's degree (Diploma) in Zoology in October 1978. The theme of the Master's thesis was: "Experiments on 'nutritional wisdom' of roe deer, *Capreolus capreolus* (Experimente zur 'Nährstoffweisheit' beim Reh, *Capreolus capreolus*).

During my biology studies I attended lectures and courses held by the following persons:
Bächli, Bachofen, Batschelet, Biegert, Brun, Burla, Chen, Christen, Claude, Cook, Eugster, Gasser, Greuter, Hediger, Hohl, Humbel, Jungen, Kägi, Keller, Kriszten, Kummer, Kündig, Nievergelt, Nöthiger, Oswald, Rast, Staub, Tardent, Turner, Wanner, Wehner, Weissmann, Woodtli, Ziswiler.

Curriculum vitae

Rusterholz, Moritz Stephan

Geboren am 30. Dezember 1949 in Zürich

Die Primarschule besuchte ich in Regensberg (ZH) und Zürich. An der Stiftung Mittelschule Dr. Buchmann in Zürich bereitete ich mich auf die Matura vor. Ab Herbst 1971 bis zum Frühjahr 1973 studierte ich Maschineningenieurwesen an der ETH-Zürich. Im Herbst 1973 begann ich mit meinem Biologie-Studium an der Universität Zürich, wo ich im Oktober 1978 die Diplomprüfung in Zoologie ablegte. Der Titel meiner Diplomarbeit lautete: "Experimente zur 'Nährstoffweisheit' beim Reh, *Capreolus capreolus*". Die vorliegende Dissertation entstand unter der Leitung von Dr. D.C. Turner.

Während meines Biologie-Studiums besuchte ich Vorlesungen und Kurse folgender Personen:
Bächli, Bachofen, Batschelet, Biegert, Brun, Burla, Chen, Christen, Claude, Cook, Eugster, Gasser, Greuter, Hediger, Hohl, Humbel, Jungen, Kägi, Keller, Kriszten, Kummer, Kündig, Nievergelt, Nöthiger, Oswald, Rast, Staub, Tardent, Turner, Wanner, Wehner, Weissmann, Woodtli, Ziswiler.